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ANGIOSPERM BIOGEOGRAPHY AND PAST CONTINENTAL MOVEMENTS¹

PETER H. RAVEN² AND DANIEL I. AXELROD³

The isolation of land areas by sea-floor spreading, the uplift of new cordilleras, the emergence of new archipelagos and the disappearance of old ones, and the shifting positions of (some) land-masses have both created and destroyed environments to which biota have responded. In this sense, changing physical environments governed by plate tectonics have had a major role in evolutionary history. Plate tectonic theory thus provides a more reliable basis for analyzing changes in land-sea relations and changes in climates, and hence for interpreting problems of evolution and distribution, than has been available earlier. The reappraisal of the nature of the earth's crust by plate tectonic theory does not require any modifications of previously established major principles of evolution. However, it does demand that we recognize certain new principles of biogeography (McKenna, 1973). Lands may be rafted across latitudinal belts of climate which may lead to *a*) widespread impoverishment of the biota (India), *b*) new opportunities for change (arid flora of Australia), or *c*) lead even to the total decimation of a rich biota (Antarctica). Since moving plates may carry ancient biota

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² Washington University and Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110.

³ Department of Botany, University of California, Davis, California 95616.

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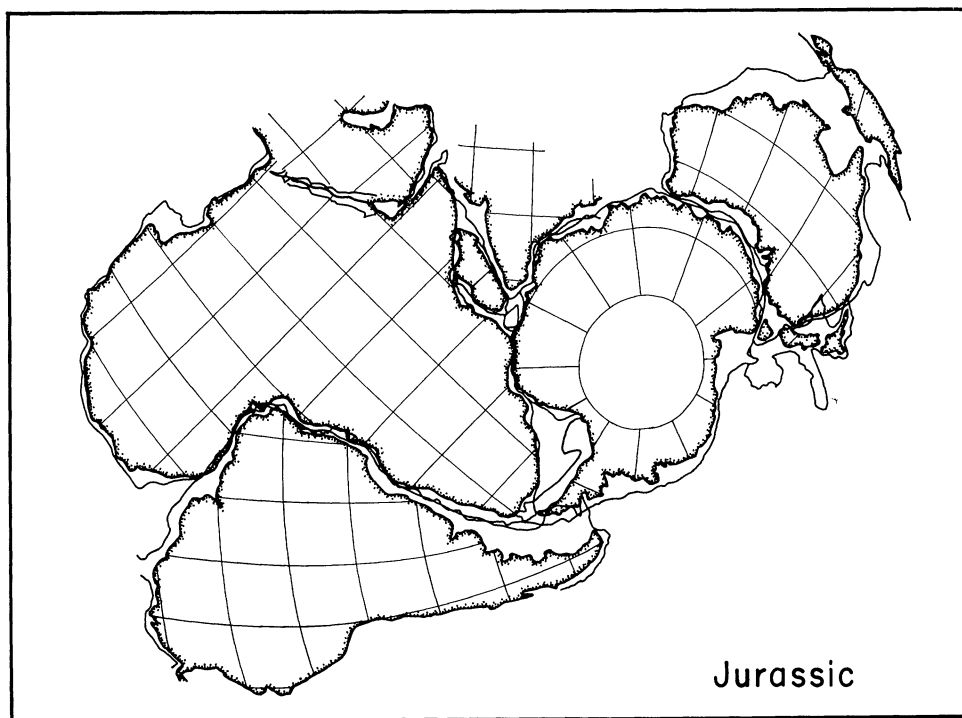


FIGURE 1. Fit of the Gondwana continents during the Jurassic, prior to breakup (after Smith & Hallam, 1970).

far from the area in which they lived, reconstructions of ancient biotic zones and climates must take cognizance of such changes

In the present paper, we examine the distributions of flowering plants, present and past, and attempt to interpret them in the light of newly available geological evidence. Although the field is vast, and we have been unable to provide a comprehensive survey of the available facts, we believe that an overview of angiosperm distributions in the light of geological history as now suggested by plate tectonic theory will be useful in suggesting new hypotheses and new directions for future research.

First, we shall review geological evidence as it pertains to certain areas that we believe were of prime importance to the evolution of flowering plants. Second, we shall review our current state of knowledge about the biogeography and history of the vertebrates of South America, critical for understanding the possibilities for migration between South America and other continents prior to the Miocene. Third, we shall attempt to interpret, insofar as possible, the timing of evolutionary radiation in the angiosperms so as to ascertain relative ages for some of the taxa. Fourth, we shall review the present distributions of the orders, families, and some infrafamilial groups of angiosperms, with selected references to the paleobotanical literature where we believe these to be useful. Fifth, we shall outline the broad patterns of angiosperm migration in the past, and interpret

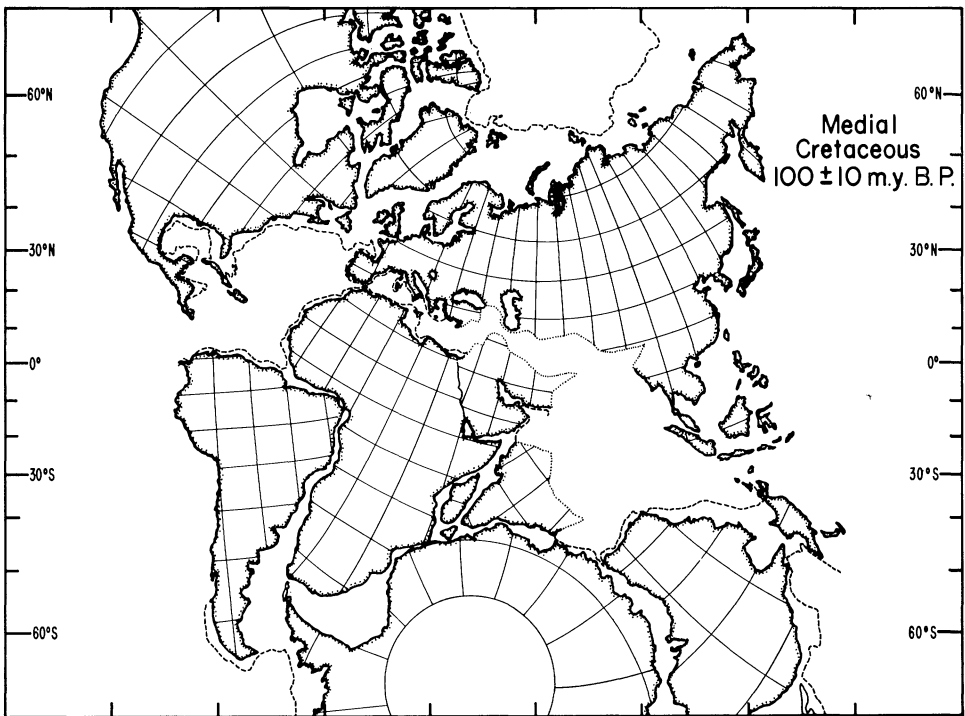


FIGURE 2. Relative positions of Laurasia and Gondwanaland in the medial Cretaceous ($\sim 100 \pm 10$ m.y. BP) (from Smith, Briden & Drewry, 1973). Note that the connection between South America and Antarctica was linear, having been deformed to make the Scotia Arc since the Cretaceous (Dalziel *et al.*, 1973).

the relationships between these patterns and the age of the respective taxa. Finally, we shall address ourselves to the question of the place of origin of the angiosperms in the light of this knowledge.

GEOLOGICAL BACKGROUND

OPENING OF THE INDIAN OCEAN

We start with a Jurassic Gondwanaland configuration like that presented by Smith and Hallam (1970; Fig. 1) or Tarling (1972). The formation of the Indian Ocean began with the rotation of Africa (with India) away from South America and the movement of Antarctica (with Australia) into a more polar position. The opening of the South Atlantic, reviewed below, began 125–130 m.y. BP. Sediments recently drilled from the ocean floor west of Australia indicate that the eastern Indian Ocean is about 150 m.y. old (Heirtzler *et al.*, 1973, footnote 13). If India was ever immediately adjacent to Australia, it separated at this time and moved westward for 80 m.y. As reviewed below, India certainly remained connected to Madagascar and Africa until at least 100 m.y. BP. Current evidence does not indicate with any degree of certainty the time of separation of Africa-Madagascar-India from Antarctica. However, in view of the configuration of the Indian Ocean 75 m.y. BP (Laughton *et al.*, 1973; Fig. 3), more or

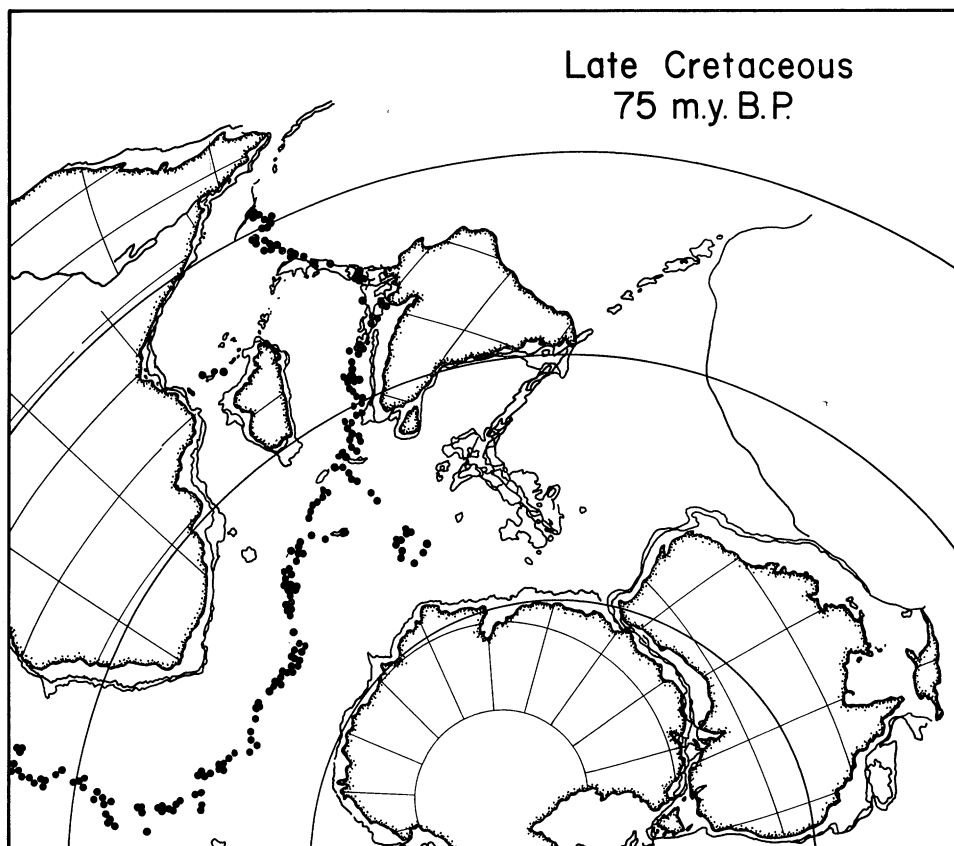


FIGURE 3. Relations between East and West Gondwanaland in the Late Cretaceous (~ 75 m.y. BP), according to McKenzie and Sclater (1971).

less direct migration between Africa and Australia *via* East Antarctica was possible into mid-Cretaceous time (Fig. 2, Smith *et al.*, 1973; see also Jones, 1972). Even if the land masses were somewhat more separated at that time, plant migration would have been easy *via* volcanic islands on mid-ocean ridges. Epi-continental seas apparently had spread around the southern and eastern coast of Africa to Madagascar by the earliest Cretaceous (Dingle, 1973), but Madagascar and India were still attached and formed a more or less continuous bridge to Antarctica and Australia into the mid-Cretaceous (Fig. 2). The initial rifting of Africa from South America, at about the start of the Cretaceous, presumably sets a limit for the earliest date for the separation of Africa-Madagascar-India from East Antarctica. See Addendum, Sclater and Fisher (1974).

Madagascar has not moved significantly relative to mainland Africa (Green, 1972; Kent, 1972), and evidently has been separated from it for as much as 100 m.y. (Simpson *et al.*, 1972; see also references summarized in McKenna, 1973). Thus many of the plants and animals of Madagascar apparently reached it across a water barrier after the mid-Cretaceous, as hypothesized by Darlington (1957).

On the other hand, the presence of sauropods in the Upper Cretaceous of Madagascar, with the genus *Laplatasaurus* reported in India and Madagascar in addition to South America, and the presence of carnosaurs also in the Upper Cretaceous of Madagascar (Charig, 1973) negates Simpson's (1973) view that Madagascar has been separated from the mainland of Africa since the Permian. A modern review of the sauropods would be highly desirable. It is possible, as reviewed by Cracraft (1973c) that India and Madagascar remained joined longer than Madagascar and Africa.

Another event of biogeographic significance is the separation of New Zealand and New Caledonia from Australia, 80 m.y. BP (summary in Raven & Axelrod, 1972). Evidently the entire Campbell Plateau region, including New Caledonia and New Zealand, had reached approximately its present position by Paleocene time, and only subsequently did Australia begin to separate from Antarctica (Houtz *et al.*, 1973; Hayes & Ringis, 1973). Normal oceanic crust began to form between the Australian and Antarctic continents about 55 m.y. BP (Weissel & Hayes, 1972; Kennett *et al.*, 1972), with the separation of the continental margins of Australia and Antarctica taking place 49 m.y. BP (McGowran, 1973). More or less direct migration through the Tasmanian area may have been possible for perhaps another 10 m.y., especially since the South Tasman Rise is now known to be continental (Houtz *et al.*, 1973; Kennett *et al.*, 1973). Present features along the Scotia Arc developed from a linear Late Cretaceous trend (Anonymous, 1972; Adie, 1972; Dalziel *et al.*, 1973), though the initial break between the Antarctic Peninsula and Tierra del Fuego, if they were ever joined (Katz, 1973), probably occurred before the Late Cretaceous (Dalziel *et al.*, 1973). The water around Antarctica was cool temperate by Late Oligocene time (Hayes *et al.*, 1973), and glaciation in Antarctica is now known to have begun at least 20 m.y. BP (Hayes *et al.*, 1973), if not earlier, with a major increase in the icecap to continental extent about 4–5 m.y. BP. There may also have been episodes of glaciation in Paleogene time (Margolis & Kennett, 1971; Denton, Armstrong & Stuiver, 1971: 271–278). More or less direct migration *via* Antarctica between Australia and South America may have continued well into the Oligocene, and was certainly possible in Eocene time (Raven & Axelrod, 1972).

It is unlikely that any portion of Southeast Asia or Indonesia was once a part of Gondwanaland and moved north, since paleontological and geological evidence contradicts such a pattern of drift (Tarling, 1972; Audley-Charles *et al.*, 1972; Stauffer & Gobbett, 1972; Ridd, 1972; Griffiths & Burrett, 1973). Not until mid-Miocene time was the migration of Asian plants and animals into Australasia relatively direct (Raven & Axelrod, 1972; Audley-Charles *et al.*, 1972).

India, which commenced its northward motion about 100 m.y. BP, now appears to have collided with Asia by the Middle Eocene (Powell & Conaghan, 1973), and there are mammal faunas of obviously Laurasian character in the Lower Upper Eocene of the Murree Hills (Ranga Rao, 1971, 1972). The extensive crustal shortening and fracturing of the region, as well as the upthrust of the Himalayas, belongs to the second phase of development of the region, commencing in the Miocene and reaching its strongest phase in Plio-Pleistocene time (Gansser, 1964, 1966; Laughton *et al.*, 1973; McKenzie & Sclater, 1973; Powell &

Conaghan, 1973). The presumed Lower Eocene Deccan Intertrappean floras reviewed by Lakhanpal (1970) may represent mixtures of groups that have come from the north (such as, perhaps, Datisceae) with those that were derived from the south, and the flora of peninsular India was progressively enriched from mid-Tertiary time onward with northern, predominantly tropical groups of angiosperms, such as Dipterocarpaceae (Axelrod, 1971).

To summarize for the lands around and east of the Indian Ocean, the following estimates are the last dates at which more or less direct migration may have been possible: 1) between West Gondwanaland and Australia, 110 ± 10 m.y. BP; 2) between Africa and Madagascar, about 100 m.y. BP; 3) between Australia-Antarctica and New Zealand or New Caledonia, 80 m.y. BP; 4) between Australia and South America *via* Antarctica, 45 m.y. BP. Direct communication between West Gondwanaland and India may have ceased about 100 m.y. BP, and direct communication between India and Asia was initiated about 45 m.y. BP.

CONNECTIONS OF AFRICA WITH OTHER CONTINENTS

The Atlantic Ocean began to open with the rotation of Africa and South America away from North America in the Early Jurassic (180 m.y. BP; Dietz & Holden, 1970; Pitman, Talwani & Heirtzler, 1971; Pitman & Talwani, 1972; Phillips & Forsyth, 1972; Walper & Rowett, 1972; Dewey *et al.*, 1973). Prior to this, Africa was also broadly connected with southwestern Europe (Smith, 1971). Beginning 148 m.y. BP and continuing until 80 m.y. ago, Africa rotated counterclockwise relative to Europe (Dewey *et al.*, 1973). During the interval 80–53 m.y. BP Africa continued its counterclockwise motion but also moved westward relative to Europe, with compressive components indicating connections until 63 m.y. BP, following which relative motion was almost entirely east-west strike-slip (Dewey *et al.*, 1973). In the Early Paleocene, Africa and Europe were connected *via* Spain. Africa may also have been connected broadly with Asia through Arabia at this time (Cooke, 1972). From the Early Paleocene (63 m.y. BP) into the Upper Eocene (53 m.y. BP), Africa and Europe seem to have become more widely separated (Dewey *et al.*, 1973, figs. 16–17), with convergence resulting in direct connection some 17 m.y. ago (Cooke, 1972; Hallam, 1973a; Dewey *et al.*, 1973). Following reestablishment of direct connections between Africa and Eurasia, many northern groups of plants and animals reached Africa, and many African taxa—for example, proboscideans and catarrhine primates—entered Eurasia.

RELATIONS WITHIN LAURASIA

As recently summarized by McKenna (1973), the European Plate (including Greenland) began to separate from the North American Plate in the Late Cretaceous (~ 81 m.y. BP; Laughton, 1971; Smith, 1971; Heirtzler, 1973), with spreading rapid until the Late Eocene and still continuing. Both the North American Mid-Continent Seaway and the Asian Turgai Strait divided the Laurasian landmass, and the Bering Strait was at a higher paleolatitude ($\sim 75^\circ\text{N}$) than at present. By 50 m.y. BP, direct migration was still possible across the North Atlantic, and the North American Mid-Continent Seaway had disappeared

by 60 m.y. BP. Since the Bering Strait was at a higher latitude, migration between Eurasia and North America across the North Atlantic was probably the main route of communication between these landmasses. Direct overland migration across the North Atlantic was possible for land vertebrates until 49 m.y. BP (McKenna, 1972), but cool temperate conifer-hardwood forests continued to occupy Iceland during the Neogene, providing an interrupted pathway between America and Europe into the early Quaternary (Schwarzbach & Pflug, 1957). Migration *via* the Bering Straits became relatively more important for land vertebrates as the North Atlantic widened and as the latitude of the Bering Straits decreased.

RELATIONS OF SOUTH AMERICA WITH AFRICA

In the South Atlantic, separation seems to have commenced 125–130 m.y. BP (Maxwell *et al.*, 1970b; Wright, 1971; Francheteau & Le Pichon, 1972; Mascle & Phillips, 1972; Phillips & Forsyth, 1972; Heirtzler, 1973; Francheteau, 1973; Anonymous, 1973; Larson & Ladd, 1973). The final marine connection associated with the spreading apart of Africa and South America took place slightly less than 100 m.y. BP (Reyment, 1969, 1972; Reyment & Tait, 1972; Douglas *et al.*, 1973), with the continents remaining in near contact along strike-slip faults until at least 90 m.y. BP (Le Pichon & Hayes, 1971; Grant, 1971, 1972), when northeast Brazil (Sergipe) and Africa (Gabon) were separated by only a narrow strait. At the close of the Cretaceous, about 800 km probably separated Africa and South America at their closest points. However, they were still linked by numerous islands which existed along the Mid-Atlantic Ridge and its flanks at that time (*e.g.* see Klerkx & de Paepe, 1971; Addendum: Anonymous, 1974).

RELATIONS BETWEEN NORTH AND SOUTH AMERICA

Relationships between the American continents during the Cretaceous Period are of great biogeographic interest. Many extant groups of organisms originated and expanded greatly during this period, and the opportunities they had for migration between the Americas have long been a subject of discussion.

North and South America have converged at least from the mid-Cretaceous to the early Cenozoic (Dietz & Holden, 1970; Freeland & Dietz, 1971; Malfait & Dinkelman, 1972). In the following remarks, however, they will be considered to have remained in their present positions, which represents a minimum estimate of distance, and therefore of ease of migration.

During most of the Cretaceous, about 3,000 km seems to have separated the southern continental margin of North America (in Oaxaca) from the continental margin of South America (the Guyana Shield; Fig. 4; Dengo, 1973). This exceeds the present distance (about 2,500 km) between Freetown, Sierra Leone, and Recife, Brazil. South America was joined to Africa until somewhat less than 100 m.y. BP, while North America was moving to the northwest; therefore, 3,000 km must be a minimum distance even if North and South America were still moving apart (*cf.* Freeland & Dietz, 1971), at least for the Early Cretaceous.

It is well established that the entire Atlantic and Gulf Coastal Plain, including Florida, was submerged in the Late Jurassic and continued to receive sediment

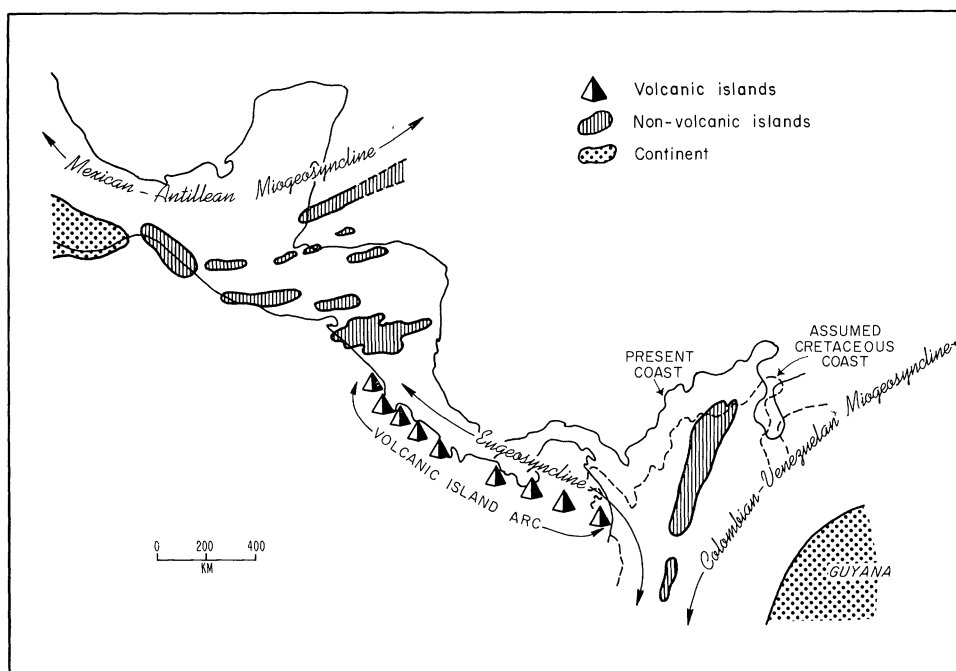


FIGURE 4. Paleogeographic relations between Central and South America in the Late Cretaceous (after Dengo, 1973).

from the Appalachians during Cretaceous and most of Tertiary time (King, 1951; Rodgers, 1970). By the Late Jurassic the distance between land at the southeastern margin of the Appalachians and the small islands along the chain of the Greater Antilles, probably was at least 1,000 km. This diminished only in the Oligocene when portions of the Coastal Plain, including Florida, began to emerge for the first time since the Jurassic (Cooke, 1945; James, 1961; Wilhelm & Ewing, 1972).

In the Late Cretaceous (Fig. 4), scattered and perhaps large continental islands were in the region of Nuclear Central America, including the Maya Mountains of Belize (Dengo & Bohnenberger, 1969) and the northern Cordillera Central in Colombia, itself probably an island. They were linked by scattered, small volcanic islands at the present site of southern Central America (Fig. 4). There also may have been a chain of scattered volcanic islands along the Greater Antilles and Lesser Antilles, leading to the continental margin of South America.

In evaluating whether this interrupted arc was an important dispersal path between North and South America, the distribution of land to the north must be borne in mind. As noted above, the southeastern margin of the Appalachians comprised the southeasternmost exposed land in North America throughout Cretaceous and Paleocene time and was separated by some 1,200 km of ocean from the volcanic islands of the Greater Antilles. The portion of North America nearest the Greater Antilles might have been an island near Honduras, itself a minimum of 650 km from Jamaica and Cuba. Apart from sea-drift moving north-

ward, scattered small islands in the Bahaman area would have enabled some long-distance migration *via* island stepping stones.

A general period of uplift at the close of the Cretaceous resulted in Nuclear Central America and the northern Andes somewhat approaching their modern configuration. From then until the start of the Miocene, migration between North and South America would have been *via* volcanic islands spanning some 1,300 km between northern Nicaragua and northern Colombia. Following the Late Eocene uplift of Yucatán, and the Oligocene uplift of the southern Atlantic Coastal Plain, interrupted migration could have occurred between North and South America *via* the West Indies. On geological grounds, this has not been as important at any time as has migration *via* Central America, and it has never been more direct than it is at present. Uplift of southern Central America that commenced in the Miocene, and continuing volcanism, gradually led to the union of North and South America about 5.7 m.y. BP.

Since the final separation of South America and Africa took place about 100 m.y. BP, and the present distance between them is about 2,500 km, it can be calculated that in the Early Eocene, South America was about equally distant from Africa and North America. Earlier, opportunities for immigration from Africa were greater; later, the connection with and possibility for immigration to North America became more direct.

The Caribbean and its Borderlands.—The geologic history of this region is exceedingly complicated and not well understood, yet it seems desirable to present a general digest of events there so that some of the historical relations of biota in the region can be evaluated more accurately.

The Caribbean Sea and Gulf of Mexico formed during the period 180–105 m.y. BP as North America moved away from South America and Africa (Freeland & Dietz, 1971, 1972; Malfait & Dinkelman, 1972; Phillips & Forsyth, 1972; Walper & Rowett, 1972). Caribbean crust probably formed *in situ*, and not as an extension of the older Pacific crust (Phillips & Forsyth, 1972; Kesler, 1973). Freeland and Dietz (1972) indicate that the formation of the Caribbean Sea began about 135 m.y. BP. By the end of the Early Cretaceous, it had opened to its maximum extent, with North and South America farther apart than at present (Freeland & Dietz, 1971, fig. 6; Malfait & Dinkelman, 1972, fig. 1; Phillips & Forsyth, 1972). The Caribbean then began to close slowly as South America moved northward relative to North America, reaching a climax in the Middle Eocene, and marked by major tectonism on both its northern and southern margins (Freeland & Dietz, 1972; Mattson, 1972).

In the region of the Greater Antilles, small islands were in the area of Cuba by the Late Jurassic (Khudoley & Meyerhoff, 1971, fig. 22). The Cayman Ridge, extending westward from the Sierra Maestra of Cuba towards Guatemala, exhibits a geology that suggests it may have been land in Paleocene to Lower Eocene time (Heezen, Dreyfus & Catalano, 1973), this then facilitating migration to Cuba and indirectly the other Antilles. The Bahamas seem to have been subsiding since initiation of drift between Africa and North America (Dietz *et al.*, 1970a, 1971; Sheridan, 1971). Most existing islands east or south of Cuba

are no older than Upper Cretaceous. Their origin probably resulted from intense crustal movements beginning in Late Aptian or Early Albian times, perhaps contemporary with the initial rifting of South America from Africa. By the Late Turonian, a chain of small- to medium-sized volcanic islands was in the area of the Greater Antilles and Lesser Antilles (*e.g.* Proto-Hispaniola, Bracey & Vogt, 1970; Puerto Rico, Mattson, 1973). However, most of the islands in both chains attained their present size and outlines only in the late Neogene.

Jamaica formed in the Early Cretaceous as a series of small volcanic islands that were uplifted substantially in the latest Cretaceous (Robinson & Lewis, 1971). However, no part of Jamaica seems to have been above sea level between Middle Eocene and the early Middle Miocene (Robinson & Lewis, 1971). This means that all of the plants and animals on Jamaica were derived by long-distance overseas dispersal since then. In this light, it is noteworthy that Jamaica has only 4 endemic genera and 784 endemic species of angiosperms (Adams, 1972), or about 27% of the native flora. By contrast, Cuba, which has not been submerged, has 41 endemic genera and about 50% endemic species (Liogier, 1962), and Hispaniola, which is younger than Cuba but has also not been submerged, has 26 endemic genera and about 33% endemic species (Howard, 1973).

In the Late Cretaceous, the Sierra Madre Occidental of Mexico was elevated and marine transgression limited to the area from Veracruz north. There was elevated land and mountains south to the present area of Oaxaca (*cf.* Malfait & Dinkelman, 1972, fig. 1; Kesler, 1973), which does not seem to have reoriented significantly relative to the mainland of Mexico since Precambrian time (Kesler & Heath, 1970).

Nuclear Central America is a Paleozoic orogenic belt extending from the Isthmus of Tehuantepec to northeastern Nicaragua (Kesler, 1971), and possibly Cuba (MacGillivray, 1970). Lateral faulting in the region does not suggest great displacement during Tertiary time (Kesler, 1971; G. Dengo, personal communication). However, some paleomagnetic evidence suggests approximately 1,000 km of northeastward displacement of Jamaica since Aptian and Albian time (Steinhauser *et al.*, 1972). Clearly, the geologic history of the region is still far from completely understood. The area from southern Mexico to northeastern Nicaragua, the Nicaraguan bank, and possibly Cuba was uplifted in the Late Cretaceous and subsequently to form what has probably remained a peninsula from Mexico to northern Nicaragua (Mills *et al.*, 1967; Dengo, 1973). The portions of Nuclear Central America that were land before the latest Cretaceous are established only for certain areas, *e.g.* the Maya Mountains of Belize (Hall & Bateson, 1972) and Honduras (Mills *et al.*, 1967). A large portion of Yucatán may have been emergent in Late Eocene time (G. Dengo, personal communication), establishing essentially the modern configuration between Cuba and Central America.

Southern Central America, extending from central Nicaragua south to the Atrato lowland in Colombia, has an oceanic basement of Senonian age overlain by younger sedimentary and volcanic rocks (Dengo, 1969). The earliest deformation is latest Cretaceous, but major uplift occurred only in Late Miocene and Pliocene times. Scattered volcanic islands existed prior to the Oligocene

(Dengo, 1967, 1968, 1969; Case, 1973), but there was no substantial land area (McBirney & Williams, 1965; Malfait & Dinkelman, 1972).

At the start of the Cretaceous, a broad zone of northern Venezuela (Bell, 1971) and much of Colombia (Schuchert, 1935; Liddle, 1946; Jenks, 1956) was subsea. Alvarez (1971) has shown that the Guajira Peninsula of Colombia was receiving sediment from a landmass to the north, perhaps at the present site of the Nicaraguan Rise. In latest Cretaceous time, the Cordillera Central of Colombia (Campbell & Bürgli, 1965; Alvarez, 1971; Anderson, 1972) and the Cordillera de la Costa of Venezuela (Bell, 1971), together with Trinidad (Barr & Saunders, 1971), emerged above the sea, the latter a large island or group of small ones (Liddle, 1946). There is evidence a landmass of considerable size, "Paría," extending from Aruba to Tobago and even Barbados, was uplifted in early Tertiary time and resulted in deposition of thick sediments to the south (Schuchert, 1935; Edgar, Ewing & Hennison, 1971). The Cordillera Oriental was elevated in late Neogene time, and reached its full height during the Pleistocene (summary in Alvarez, 1971), giving the land area of northwestern South America its present configurations. The complex history of the Sierra Nevada de Santa Marta has been treated by Tschanz *et al.* (1974).

From the Early Oligocene onward, volcanic islands along the present axis of Central America gradually coalesced into continuous land. About 10–12 m.y. ago there was evidently an intermittent land connection to Panama from the north (Whitmore & Stewart, 1965; Malfait & Dinkelman, 1972), which finally coalesced to join North and South America about 5.7 m.y. BP (Simpson, 1950; Kaneps, 1970; Haffer, 1970; Graham, 1972a; Emiliani, *et al.*, 1972).

Summary.—Judging from the geology of the region, and the relative motions of the plates, South America was more accessible to immigration from Africa than from North America until after the Early Eocene. Subsequently, more and more insular connections with North America were established, culminating with a direct land connection only 5.7 m.y. BP. Clearly, the history of South American biota has been one of evolution in isolation of an initial West Gondwanaland stock shared with Africa. To South America have come many cool temperate Australasian plants and animals, essentially overland until the Eo-Oligocene, and by overseas long-distance dispersal subsequently. South America contributed increasingly to the flora of tropical and subtropical North America during the Tertiary, it received immigrants from temperate North America only as the Cordillera rose in the late Neogene, at which time it also contributed montane tropical taxa to Central America.

SUMMARY OF PLATE TECTONIC EVENTS

The following events have had great importance for the patterns of evolution and distribution of organisms: (1) Direct migration last possible between North America, Europe, and Africa, 180 m.y. BP. (2) Direct migration last possible between West Gondwanaland (Africa + South America) and Australasia for warm-temperate and subtropical plants and animals, 100 ± 10 m.y. BP. (3) Direct migration between Africa and Madagascar, and probably also India, last possible, about 100 m.y. BP (possibly more recent; evidence ambiguous). (4)

Overland direct migration last possible between South America and Africa, nearly 100 m.y. BP. (5) Direct migration between Australia and New Caledonia–New Zealand, 80 m.y. BP. (6) Last direct connection between Africa and Eurasia prior to the Miocene, ~ 63 m.y. BP. (7) Direct migration possible across the North Atlantic for plants throughout the Tertiary, but for land animals until 49 m.y. BP, when the Bering Straits became more and more important as a migration route. (8) South America equally distant from North America and from Africa, ~ 50 m.y. BP. (9) India abuts against Asia, ~ 45 m.y. BP. (10) More or less direct migration possible between South America and Australia *via* Antarctica until approximately 38 m.y. BP. (11) Reestablishment of direct connection between Africa and Eurasia, 17 m.y. BP. (12) More or less direct migration first possible between Asia and Australasia *via* New Guinea, ~ 15 m.y. BP. (13) Direct land connection between North and South America, 5.7 m.y. We shall now proceed to consider existing and past patterns of distribution among vertebrates and flowering plants in relation to these events.

BIOGEOGRAPHY OF SOUTH AMERICAN VERTEBRATES

Although we shall devote our attention chiefly to vascular plants, we shall first review the present state of understanding of vertebrate history in South America. We do this for precisely the same reasons that the entomologist Darlington (1957) selected the vertebrates as the primary material for his volume on zoogeography. Vertebrates, both Recent and fossil, are better known than any other group; the patterns of distribution that they display should parallel those found in other groups of organisms, and it should be simpler to look among the vertebrates for solutions to many outstanding problems that are evident in the distribution of other organisms. Furthermore, the basic hypotheses and the amount of evidence that were utilized in Darlington's (1957) synthesis are now so out of date it is necessary to review the facts again in a more modern context. Our remarks supplement the reviews presented by Cracraft (1973*b*, 1973*c*).

In preparing the present paper, we have consulted a number of treatments of invertebrates and cryptogams, such as those presented in the two volumes on biogeography and ecology in South America (Fittkau *et al.*, 1968, 1969), and find their patterns of distribution to accord, in general, with those of the vertebrates and vascular plants upon which we shall focus here. A particularly elegant analysis of an exactly parallel pattern has been presented by Edmunds (1972) for the mayflies, and Schlinger (1974) has recently provided interesting new information on the insects associated with *Nothofagus*.

We shall now analyze the paleobiogeography of each of the groups of vertebrates in turn.

FISHES

The dominant freshwater fishes of Africa and South America are characoids and siluroids, both derived from ancestral forms that dispersed directly between these continents when they were united (Myers, 1966; Roberts, 1973, Fig. 1, 3). In South America, the characoids gave rise to the endemic gymnotids, and in Africa cyprinoids subsequently entered from the north (Gosline, 1972), probably

at least in part in Neogene time. There are thus no gymnotids in Africa and no cyprinoids in South America. The non-ostariophysan primary freshwater fish families of South America, Lepidosirenidae, Osteoglossidae, and Nandidae, are all shared with Africa. No primary freshwater fishes of North American origin extend south of Lago Nicaragua, and none has reached South America (Myers, 1966), contrary to the elaborate scheme proposed by Darlington (1957). The dominant cichlids and poeciliids of Central America are secondary freshwater fishes that disperse across saltwater barriers. The cichlids probably were derived from South American forms, whereas the poeciliids may have been derived from North American cyprinoids. Both evidently have been radiating in Central America through most of Neogene time. No primary freshwater fish from South America reached Central America until these lands were connected, about 5.7 m.y. BP. Subsequently, a few genera of characoids extended their range north into Mexico, and one (*Astyanax*) reached the Rio Grande (Myers, 1966). The evidence from the distribution of freshwater fishes is in full accord with our present understanding of the relationships between Africa, South America, and North America.

AMPHIBIANS

Caecilians, recently reported from the Late Paleocene of Brazil (Estes & Wake, 1972), almost certainly dispersed overland between South America and Africa in the Cretaceous or earlier, and also spread between Africa and Asia. Salamanders are a Laurasian group, with plethodontids having reached South America from North America after the establishment of a direct land connection between them in the late Neogene.

Frogs may have originated in Gondwanaland, though the suggestion must remain speculative (Laurent, 1972; Estes & Reig, 1973: 48; Reig, 1973). At any rate, South America together with Africa (= West Gondwanaland) has clearly been the primary area from which most, if not all, modern lines of anurans have been derived (Savage, 1973). Pipidae almost certainly dispersed directly between Africa and South America. They are known from the Late Cretaceous of both regions, and from the Early Cretaceous of Israel (Laurent, 1972; Estes & Reig, 1973). Bufonidae (including Atelopidae) may also have done so (Cracraft, 1973b). Since *Heleophryne* of southern Africa is a leptodactylid (Lynch, 1971), it seems reasonable that the group dispersed directly between South America and Africa prior to their separation, and also across Antarctica to Australia (Darlington, 1957: 166; Lynch, 1971). However, Cracraft (1973b) points out that relationships with the Northern Hemisphere pelobatids and phylogenetic lines within the leptodactylids must be understood better before definite conclusions can be drawn.

Savage (1973) contends that one of the genera of Leptodactylidae (*Eleutherodactylus*) reached North America prior to the Pliocene. Savage (personal communication) has pointed out that *Eleutherodactylus* sens. lat. is an excellent candidate for overwater dispersal, with an encapsulated, land-laid egg, like the widely distributed ranid *Cornufer* (*Platymantis*), which has reached Fiji. There are approximately a hundred species of *Eleutherodactylus* in the West

Indies, and at least three derivative endemic genera—*Sminthillus*, *Syrrhophus*, and *Tomodactylus*—are north of South America.

Leiopelmidæ, known as fossils in the Mesozoic of South America (Estes & Reig, 1973), occur today only in northwestern North America and New Zealand. Dispersal to New Zealand need not be explained *via* Antarctic connections. Since this group is known from the Early Jurassic, it may have spread directly between any of the continents (see Fig. 1), and may have arrived in North America much earlier than suggested by Estes and Reig (1973: 47).

Hyla is evidently a South American derivative of leptodactylid stock (Savage, 1973: 414). The Central American hylids are derived from South America, whereas the Nearctic hylids are more closely related to Eurasian taxa (Duellman, 1970). The recent record of *Hyla* from the Early Oligocene of Saskatchewan (Holman, 1969, 1972) implies sweepstakes dispersal from South to North America at least that early, whereas contemporary Central American hylids evidently came later. Although *Hyla*, using some current concepts, would seem to have migrated from South America to Australia directly (Raven & Axelrod, 1972), Tyler (1971) and Savage (1973: 356) have recently allied Australasian forms currently referred to *Hyla* to leptodactylids. This implies their independent derivation from other leptodactylids in Australia.

Bufo, first known from the Paleocene of Brazil (Estes & Reig, 1973), also seems to have been derived from leptodactylid stock in South America (Blair, 1972), spreading by sweepstakes dispersal to North America (Blair, 1972, Fig. 18-1). The presence of fossil bufonids in the Eocene of Europe (R. Estes, personal communication) implies their arrival in North America at least that early, even though the first fossils are from the Lower Miocene. The ancestors of the African groups, which are distinctive, might have arrived by rafting in the Paleocene across a much narrower South Atlantic (*cf.* Laurent, 1972), as we shall discuss below for primates and caviomorph rodents. Blair (1972) has emphasized the similarity between *Bufo* species in Africa and South America. *Rana* reached South America very recently, *via* North America from Eurasia (Darlington, 1957: 170).

To summarize, caecilians and several groups of anurans seem clearly to have migrated overland between South America and Africa in the Cretaceous. *Hyla* probably reached North America from South America by the Early Oligocene at least, and a number of other groups were exchanged between these two continents in the Miocene and more recently. There is no evidence that any amphibians passed directly between North and South America between Lower Jurassic and Early Oligocene times, although the presence of bufonids in the Eocene of Europe suggests that they may have done so.

REPTILES

The four families of dinosaurs recorded from the Upper Cretaceous of South America all occur in North America, and only one has been recorded definitely from Africa (Charig, 1973). These relationships have been used to argue that migration between North and South America must have been relatively direct at that time, and that migration between South America and Africa very indirect

(Colbert, 1952; Darlington, 1957; Charig, 1973). Of these four families, however, one is doubtful in South America and a second has been doubtfully recorded from Madagascar. Ceratopsidae, abundant in North America, are known in South America only from a single fragment of a lower jaw from the Upper Cretaceous of Argentina, which is very doubtfully assigned to this family (Colbert, 1948). Hadrosaurs, abundant in North America at the same time, have not been found in the Southern Hemisphere. Finally, at the generic level, as among the nearly cosmopolitan sauropods, there is as strong an indication of connection between South America, Africa/Madagascar, and India as between East Asia and North America (Charig, 1973).

This analysis of dinosaur distribution, therefore, does not support the notion of direct migration between North and South America in the Mesozoic, which agrees with the known positions of Africa and South America in Early Cretaceous time. There is, however, ample evidence of links between South America, Africa, India, and Madagascar, probably until Upper Cretaceous (Charig, 1973; Colbert, 1973). Cetiosaurinae are known from the Jurassic of Australia, Coeluridae (Charig, 1973), Megalosauridae (Colbert & Merrilees, 1967), and Iguanodontidae (E. H. Colbert, personal communication) from the Early Cretaceous. The presence of these large dinosaurs certainly indicates terrestrial connections between Australia and other parts of the World at that time (Colbert, 1973). However, all of these families existed in the Jurassic, and they might have arrived in Australia prior to the close of that period.

Among the turtles (Simpson, 1943), the pelomedusids evidently dispersed between South America and Africa when these were linked or close to one another, and fossils are known from both regions, as well as from the Northern Hemisphere (Darlington, 1957). Land tortoises (Testudininae) and Chelydridae may have reached South America from North America in the Miocene or more recently, and the Emydinae, basically a northern group, probably did the same. Most other groups are basically northern or southern. Before the arrival of the predominant northern groups of turtles in South America in Neogene time, there were meiolaniids and chelyids, both of which may have reached Australia *via* Antarctica (Raven & Axelrod, 1972). There is no evidence for dispersal of turtles between North and South America prior to Miocene time.

Of the lizards, Iguanidae first appear in the fossil record in the Upper Cretaceous of Brazil (Estes & Price, 1973). The diversity of Paleocene iguanids there suggests that the evolution of the family took place primarily in South America (Tihen, 1964; Estes, 1970). They appear in North America, which they probably reached by sweepstakes dispersal, in the Eocene. The presence of two relict genera on Madagascar suggests that iguanids passed from South America to Africa-Madagascar in the Cretaceous (Estes & Price, 1973). The occurrence of a third endemic genus on Fiji and Tonga seems to be related to long-distance trans-Pacific dispersal, presumably *via* archipelagos, since it is closely related to the American genus *Iguana* (R. Estes, personal communication).

Gekkonidae probably also dispersed more or less directly between South America and Africa during the Cretaceous (Cracraft, 1973*b*). Teiidae seem to have been in both North and South America in the Late Cretaceous (Estes, 1970) and probably spread to North America by sweepstakes dispersal at that time.

However, the only Recent teiid north of Mexico, *Cnemidophorus*, which undoubtedly came from South America, first appears in the North American fossil record in the Early or Middle Miocene (Estes, 1963; Estes & Tihen, 1964; Tihen, 1964). For Amphisbaenidae, now known chiefly from South America and Africa, the Paleocene fossil record in Eurasia and North America suggests a route from Africa to Europe and then to North America. Summarizing, teiids seem to have reached North America from South America by sweepstakes dispersal in the Upper Cretaceous, iguanids in the Eocene, and many other groups of lizards in the Miocene and subsequently.

Aniliid and boid snakes extend back to the Late Cretaceous (Estes, Berberian & Mesozoely, 1969; Estes, 1970), and more primitive snakes are in the Early Cretaceous (Hoffstetter, 1959). The boa *Madtsoia*, if correctly identified, is known from the Upper Cretaceous of Madagascar and the Paleocene-Eocene of Patagonia (Del Corro, 1968). Hence, some boids and possibly other primitive snakes dispersed more or less directly between Africa and South America. Tertiary boids known from North America may have arrived *via* Europe, and snakes must have reached Eurasia prior to the Early Paleocene. Colubroid snakes, which have diversified in the main Eurasian landmass (Rabb & Marx, 1973), reached South America from North America in the Miocene (Hoffstetter, 1967), and have undergone extensive radiation there subsequently. Their diversity in South America in itself seems to be insufficient evidence to postulate an antiquity there greater than the Miocene, contrary to the arguments of Raab and Marx (1973). The early evolution of tropical American colubroid stocks may have taken place in southern North America (= Central America), where Savage (1966) has demonstrated the presence of a substantial endemic element, presumably of some antiquity, among the reptiles. As for Australasia, it is unlikely that any snakes, except possibly seasnakes, reached the area prior to the Miocene, because the Australian snake fauna consists of groups not known to have been in existence prior to the Tertiary.

MAMMALS

As summarized by Clemens (1968, 1970), marsupials are known from the Albian (> 110 m.y. BP; but see Cox, 1973) to the Early Miocene of North America, the Early Eocene to Miocene of Europe, and are also reported from the Upper Cretaceous of Peru (Grambast *et al.*, 1967; Sigé, 1971). They have persisted to the present in South America, and *Didelphis* colonized North America in the Pleistocene, subsequent to the formation of a land connection, reestablishing marsupials in the north after an absence of some 20 m.y. The predominantly southern distribution of marsupials renders it probable that they originated in West Gondwanaland, dispersing directly to Australia (Raven & Axelrod, 1972; Keast, 1972; Cox, 1973). Didelphoids had reached North America by the Upper Cretaceous and were in Europe at least by the Early Eocene. Fossil marsupials are not known from Africa but may be expected there. They spread between North and South America either by sweepstakes dispersal (more likely if they were spreading near the end of the Cretaceous) or *via* Africa and Europe (which can only be confirmed if and when fossil marsupials are discovered in the Cretaceous of Africa and Europe; Cox, 1970; Fooden, 1972). If the Mongolian

Deltatherium proves to be a marsupial (Butler & Kielan-Jaworowska, 1973), the group would then be demonstrated to have been present in Eurasia in Santonian-Campanian time.

Monotremes, like dinosaurs, presumably reached Australasia overland *via* India in the Lower Cretaceous or even Jurassic. Although inferential and some direct evidence suggests the presence of prototherians (monotremes), metatherians (marsupials), and eutherians (placentals) in West Gondwanaland before the separation of Africa and South America, eutherians do not appear to have been in the region early enough for direct migration to Australasia, as discussed below.

One family of notoungulates, Arctostylopidae, is known only from the Upper Paleocene of Mongolia and the Upper Paleocene and Lower Eocene of North America (Simpson, 1945; M. C. McKenna, personal communication). Since other families of the group are exclusively South American, and it seems most likely that notoungulates ancestral to Arctostylopidae reached North America by sweepstakes dispersal from South America by the close of the Paleocene, thence *via* the Bering Straits to Asia. However, an indirect route from West Gondwanaland *via* Eurasia to North America is not precluded.

How the condylarths passed between North and South America is unknown (Kurtén, 1973). The group is not known from African fossils and presents an enigma comparable with that of the marsupials.

Darlington (1957), following Simpson (1945), places the Metacheiromyidae with the edentates, and says that the nearly complete skeletons of *Metacheiromys* are "among the most important of all fossil mammals," because they show that "early in the Tertiary, edentates were in North America, from where they may have reached South America" (Darlington, 1957: 383). Emry (1970) has since shown that the Metacheiromyidae are not edentates but members of the Pholidota. The edentates are therefore an exclusively austral group that spread to North America in the Pliocene.

Among other groups of mammals, caviomorph rodents and platyrrhine primates appear in the fossil record of South America in the Early Oligocene (Patterson & Pascual, 1972). Perhaps the ancestors of both groups arrived by rafting and island-hopping from Africa (Hoffstetter, 1972): in the Early Oligocene South America appears to have been about equally distant from North America and from Africa. Since a platyrrhine primate reached Jamaica in the Pliocene or Pleistocene over a water barrier of about 600 km, perhaps a gap of about twice that distance from Africa to South America was crossed in the Eocene. Hystricomorphous and hystricognathous rodents are known from the Eocene of Europe and North America (Wahlert, 1973), and there is one additional recent record of a hystricognathous rodent from the Eocene of North America (Wood, 1972). Otherwise, living hystricomorphous rodents occur in Eurasia (Old World porcupines only), Africa, and South America, with a Pleistocene invasion of North America by one group of New World porcupines, *Coenodon*. The New World hystricomorphous rodents, almost entirely South American, are all caviomorphs, a group that does not occur in the Old World. The known Eocene North American hystricomorphous and hystricognathous rodents clearly are not ancestral to the caviomorphs (Wood, 1972; Wahlert, 1973, and personal communication),

and presumably evolved in North America from a mammalian fauna that was shared with Europe. Thus the derivation of the caviomorph rodents in South America may have been from ancestral forms that arrived from Africa, as mentioned above, and hystricomorph rodents provide no evidence for direct migration between North and South America until the Late Pliocene. The same is true for platyrrhine primates, which seem to have reached Central America and the West Indies only in Pliocene time, and subsequently.

Marsupials and condylarths might have dispersed between North and South America in the Cretaceous (Keast, 1972), but the evidence is not strong and the assumption is based mainly upon contemporary geography. The extensive exchange of mammalian faunas between North and South America which began about 5 m.y. BP is, of course, well established (Simpson, 1947*a*; Patterson & Pascual, 1972; Savage, 1973). However, there is no evidence for an earlier "intense exchange of land mammals" (Darlington, 1957: 365), and none would be expected from the geological history of Middle America. Before the extinct *Cyonasua* group of extinct procyonids arrived in South America in the Middle Pliocene, Arctostylopidae provide the only convincing case for direct dispersal between North and South America, although marsupials and condylarths might also have crossed the gap between these two continents. These facts argue compellingly for the absence of any direct, or even relatively direct, connection for mammals between North and South America until latest Neogene time.

It appears probable that the original mammalian stocks of South America (condylarth-ungulates and edentates) were derived from an Early Cretaceous mammal fauna shared with Africa (Hoffstetter, 1972). Unfortunately, nothing is known about the Cretaceous mammals of Africa, and we have only fragmentary knowledge about those in the South American Cretaceous. The earliest known African Tertiary mammals, from the Late Eocene, are highly endemic and all proboscideans (Coryndon & Savage, 1973; Cooke, 1973).

BIRDS

Although birds disperse readily across many sorts of barriers and have a poor fossil record, their patterns of distribution accord with those of other groups (Darlington, 1957; Cracraft, 1973*b, c*). Cracraft (1973*b, c*) has suggested that such families as Struthionidae, Musophagidae, Coliidae, Pteroclididae, Columbidae, Psittacidae, and Eurylaimidae and indeed such orders as Columbiformes, Galliformes, Psittaciformes, and Cuculiformes, may have radiated from West Gondwanaland, and the ratites as a whole may also have done so (Raven & Axelrod, 1972; Cracraft, 1973*c*). A number of important Oriental and otherwise cosmopolitan families of birds, such as Psittacidae and Columbidae, are especially well developed in Australasia. South America is a rich center of diversity for the latter two families and many others which apparently diversified there during the Late Cretaceous and Tertiary.

The absence of living or fossil ratite birds in North America and the presence of a distinctive tropical North American (including Central American) bird fauna, perhaps including such families as Motmotidae, Todidae, Cracidae, Trochilidae, and Thraupidae (Mayr, 1946, 1964; Bond, 1948; Cracraft, 1973*c*),

reemphasize the wide separation of North and South America in Paleogene times. In attempting to minimize this relationship, Darlington (1957: 279–287) confused the issue by assuming that Central America was an island lying between North and South America.

Although no confirmation is possible on the basis of present fossil evidence, the primary radiation of the birds as a group may well have taken place in West Gondwanaland, with migration to the Northern Hemisphere from Africa to Europe by the Late Jurassic. Judging from the pattern found in many other groups and discussed later in this paper, numerous phylogenetic lines became extinct in Africa after its separation from South America, and this, together with its ready access to Eurasia, may account for the low degree of endemism in Africa noted by Cracraft (1973*b*), as may the impact of spreading aridity (see p. 608).

Summary.—Direct dispersal between Africa and South America prior to Santonian time (80–85 m.y. BP) is evident for many tropical groups which basically have a West Gondwanaland pattern of distribution. These include characoid and siluroid primary freshwater fishes, as well as the fish families Lepidosirenidae, Osteoglossidae, and Nandidae; caecilians and at least two families of anurans, Pipidae and Leptodactylidae; pelomedusid turtles; iguanid and amphisbaenid lizards; boid snakes; several groups of dinosaurs; and ratite birds. It is probable that the condylarth-ungulate and edentate stocks of South America were derived from a Cretaceous mammal fauna shared with Africa, and that the primary radiation of anurans, birds, marsupials, snakes, and lizards also took place on this large tropical landmass.

Direct migration between Africa and Eurasia was possible at various times during the Cretaceous and Paleocene, and direct migration between Europe and North America was easily possible for vertebrates until the Early Eocene (~49 m.y. BP). However, it is uncertain whether such animals as marsupials, amphisbaenid lizards, boid snakes, and various dinosaurs passed between North and South America *via* Africa and Europe, or directly. A better understanding of the fossil record, and a clarification of the affinities of extinct members of these groups, may lead to the solution of this problem for at least some of the groups. At any rate, present evidence suggests that the following groups of vertebrates probably did pass *via* sweepstakes dispersal between North and South America by the times indicated: (1) teiid lizards, Late Cretaceous; (2) arctostyloid mammals, Upper Paleocene; (3) the genus *Bufo* and iguanid lizards, Eocene; (4) the frog genus *Hyla*, Early Oligocene. Marsupials and condylarths may have dispersed between the two continents in the Cretaceous, but otherwise the five groups mentioned above constitute the only likely instances of dispersal by land vertebrates between North and South America in Cretaceous and Paleogene times.

Considering the rich and varied vertebrate faunas of North and South America, the small amount of interchange certainly accords with the geological evidence that suggests a very wide separation of the Americas in Cretaceous and Paleogene time. In the Miocene and subsequently, interchange between the two continents of the Western Hemisphere accelerated and led eventually to the development of a Latin American fauna. The rich and endemic flora and fauna of South

America, however, evolved principally during its period of isolation from both Africa and North America, a span of some 70 m.y. between the Santonian (Upper Cretaceous) and the late Neogene. West Gondwanaland, a large landmass lying in tropical latitudes and more or less united until about 90 m.y. BP, seems to have been the primary seat of evolution and radiation of many groups of plants and animals, with intermittent migration to the north *via* Africa; a cool temperate connection to Australasia until about 45 m.y. BP; and an increasingly effective direct interchange between South America and North America during approximately the last 10 m.y.

THE BIOGEOGRAPHY OF ANGIOSPERMS

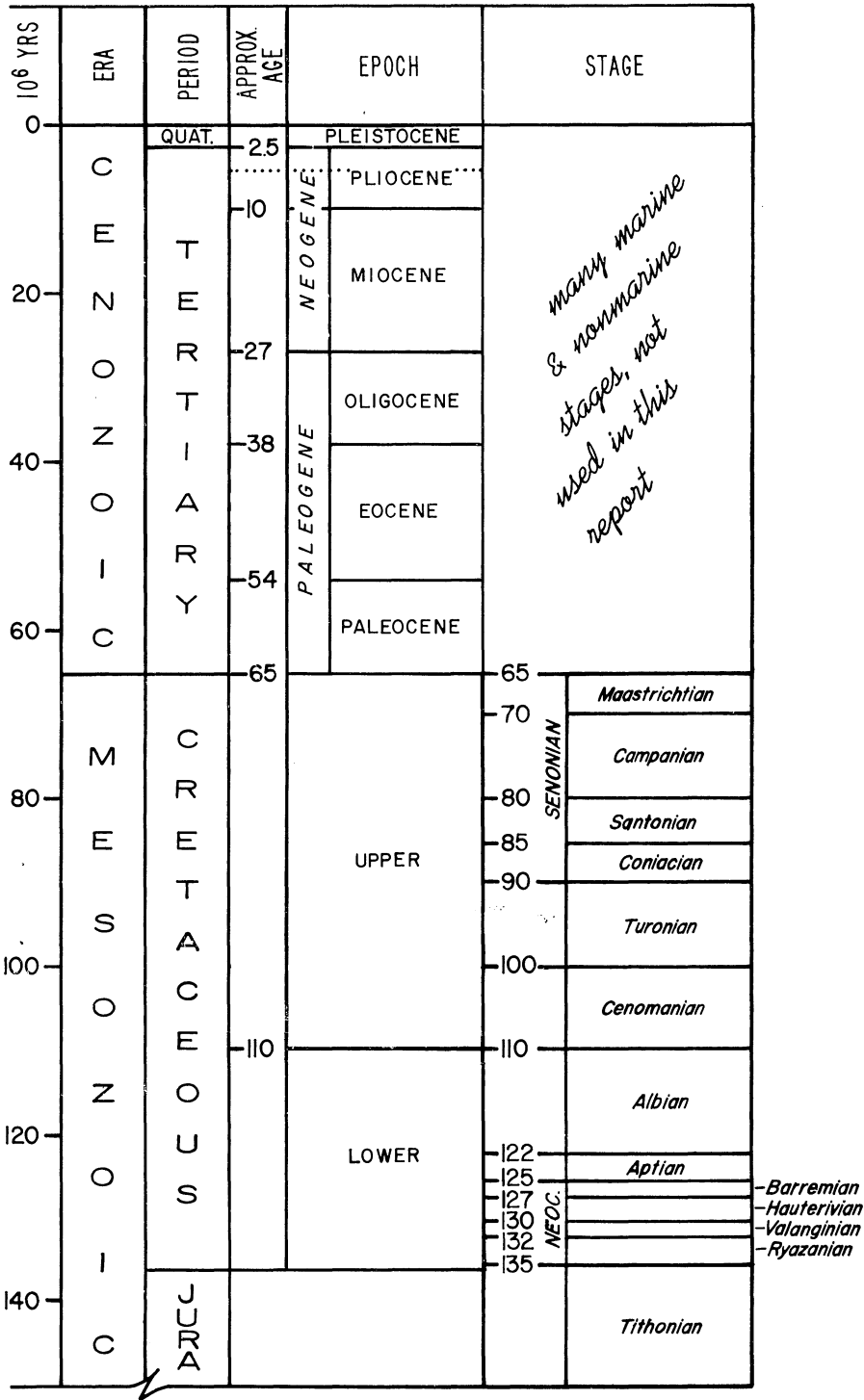
In the light of the geological evidence reviewed above, and the patterns of evolution and migration that can be seen among living and fossil vertebrates, we shall now review the patterns of distribution among the flowering plants. In order to establish the relevance of certain dates to the history of the groups concerned, we shall first briefly review what is known about the timing of major differentiation among the angiosperms.

THE AGE OF THE ANGIOSPERMS

Although the group might be considerably older, and have existed in low numbers (Axelrod, 1952*b*, 1970), undoubted monosulcate angiosperm pollen is first known from the Barremian of England, Maryland, and Argentina (Couper, 1964; Archangelsky & Gamero 1967; Kuprainova, 1967; Kemp, 1968; Doyle, 1969; Muller, 1970; Brenner, 1974; Wolfe *et al.*, 1975). Such pollen is characteristic of the Annonales ("woody Ranales") and Nymphaeales among the dicots and of the monocots, which were definitely distinct by Aptian time (Samylina, 1968; J. A. Doyle, 1973). Tricolpate pollen, characteristic of all dicots other than Annonales and Nymphaeales, is first reported from the Hauterivian to Barremian of the U.S.S.R. (Bolchovitina, 1953; Pokrovskaya, 1964; Voronova, 1966); these records have not been reconfirmed, as far as we are aware, in the more recent literature. It is next recorded from Barremian-Aptian beds in the Northern Negev of Israel (Brenner, 1974), and from the Aptian of Brazil (Muller, 1966; Brenner, 1974), the U.S.S.R. (Yedemskaya, 1960; Panova, 1964; Voronova, 1966; Khlonova, 1971; Orlova-Turchina, 1971; Papulov, 1971), and the U.S.A. (Hedlund & Norris, 1968; J. A. Doyle, personal communication). The information available at present is indecisive about the place of origin of plants with tricolpate pollen (Jones & Kremp, 1973; R. E. Jones, personal communication). An origin in tropical West Gondwanaland, attractive on ecological grounds, would be consistent with these data (Brenner, 1974). Tricolpate pollen does not appear in the record in Arctic North America until Cenomanian time, this certainly being in accordance with

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FIGURE 5. Geological time scale since the Jurassic. The ages of most of the Epoch/Stage boundaries are correct to within 1–2 million years, as judged from radiometric dates. Some authorities (Berggren, 1972; Kaneps, 1970; Van Couvering & Miller, 1971) have shown that the Miocene-Pliocene boundary in the *marine* section may be as young as 5.5 m.y.; see dotted line). For Cretaceous time see Addendum: Baldwin *et al.* (1974). Neoc. = Neocomian.



the notion of a northward migration of early angiosperms from middle latitudes (Hughes, 1961, 1973; Doyle, 1969; Brenner, 1974), as suggested earlier on the basis of megafossil evidence by Axelrod (1959). See Hopkins (1974) in Addendum.

Among the few putative pre-Aptian megafossil records of angiosperms is *Onoana*, from the Hauterivian of northern California (Chandler & Axelrod, 1961), which is very likely a gynospermous seed (Wolfe *et al.*, 1975; M. E. J. Chandler, personal communication).

Chandler (1958) recorded a structure of uncertain affinity that she regarded as an angiosperm fruit from the Valanginian of France, but the specimen has not been traced since World War II and its identity is uncertain (M. E. J. Chandler, personal communication). Various pre-Campanian palmlike leaves such as the Jurassic *Propalmophyllum* and the Triassic *Sanmiguelia* are not now generally regarded as palms (Read & Hickey, 1972; Scott *et al.*, 1972; Moore, 1973; Doyle, 1973). An example of a pre-Cretaceous fossil which exhibits certain angiosperm-like tendencies (reduction in seed size, pappus-like parachute) is Upper Jurassic *Problematospermum* (Krassilov, 1973).

There are few suggestions of Aptian (122–125 m.y. BP) angiosperm diversity in the available record. Krassilov (1967, 1973) has assigned fruits from the Aptian of Primorye in the Far East of the U.S.S.R. to *Onoana*, but his description “probably many seeded, and spiny” (1973: 172) suggests they represent a very different taxon. Krassilov simply interprets it as a primitive angiosperm and apparently associates with it Upper Cretaceous staminate heads with pollen of the *Tricolpopollenites* type which is not recorded before the basal Albian.

By Upper Albian time (110–113 m.y. BP), diverse angiospermous floras existed, as shown for the Potomac Group (Wolfe *et al.*, 1975); the Dakota flora, that from the Cheyenne Sandstone (Lesquereux, 1891; Berry, 1922; most, if not all, of the generic determinations are incorrect); and other contemporary floras. Small tricolpate pollen with a psilate or finely reticulate sculpturing becomes abundant in the Middle Albian at many widely scattered localities at middle latitudes (Brenner, 1974), but was already widespread by Aptian time, as we have seen. On present evidence, it appears reasonable that primitive members of the Annonales and of one or more groups of monocotyledons were in existence by Neocomian time, at the latest. The tricolpate pollen which appears in the record in the Aptian may be compared with that characteristic of some modern families, but the picture is blurred (Doyle, 1969; Muller, 1970). In any event, such groups as Annonales, Theales, Berberidales, and Hamamelidales, or their immediate precursors, as well as some monocots (see also Samyline, 1968: 216; Doyle, 1973), might logically be considered to have existed before the close of the Lower Cretaceous and possibly considerably earlier.

Although more diversity appears in the pollen record in the Cenomanian, it is in general not until the Turonian and Senonian that angiosperm pollen becomes more abundant than the spores of ferns and the pollen of gymnosperms, with a concomitant great increase in angiosperm diversity. The number of modern angiosperm families recorded for the Cenomanian has apparently been greatly exaggerated by superficial comparisons of leaves and fruits with those of modern taxa (Penny, 1969; Muller, 1970). By Maastrichtian time, however, a number of

modern genera and families were definitely present (Muller, 1970; Wolfe *et al.*, 1975; Wolfe, 1974). These include *Nypa* (Arecaceae), *Ctenolophon* (Linaceae), Proteaceae, Myrtaceae, *Ilex* (Aquifoliaceae), Poaceae, Sapotaceae, *Nothofagus* (Fagaceae), *Pachysandra* or *Sarcococca* (Buxaceae; Srivastava, 1972), *Ascarina* (Chloranthaceae), *Anacolasia* (Olacaceae), *Alnus* (Betulaceae), *Guarea* (Meliaceae; Graham, 1962), and *Symplocos* (Symplocaceae), as judged by very strict criteria (Muller, 1970). It is reasonable to infer the existence of some modern families by Turonian time (90–100 m.y. BP) and at least several orders in the Cenomanian, with some even earlier. By the Paleocene, *Alyxia* (Apocynaceae), *Betula* (Betulaceae), *Barringtonia* (Lecythidaceae), *Brownlowia* (Tiliaceae), *Bombax* (Bombacaceae), *Crudia* (Caesalpinaceae), and *Liquidambar* (Hamamelidaceae) were in existence, as were very many other living genera (*e.g.* see Brown, 1962).

This pattern of appearance of angiosperms in the lowland record suggests that the primitive members of several extant orders and perhaps even a few families were already in existence by the close of the Early Cretaceous, 110 m.y. BP. Many more were in existence when essentially direct interchange was still possible between Africa and South America, 90 m.y. BP, and a great many by the Paleocene when these two continents were only about 800 km apart and linked by numerous volcanic islands. Most modern angiosperm families were in existence before the connection between Africa and Eurasia was severed in the Paleocene, about 63 m.y. BP. All but the most recently derived families had originated when direct migration between Australia and South America was still possible, ~45 m.y. BP, although this path was used only by cool-temperate organisms. Many of the ancient angiosperms and animals of Australasia presumably did not come by this temperate pathway from South America prior to the Cenomanian, but directly from West Gondwanaland *via* India and Antarctica (see Fig. 2). Similarly, the ancient tropical and subtropical flora and fauna of South America was shared with Africa, and has been enriched only in the later Neogene and more recently with temperate North American taxa in ever-increasing numbers. It now remains to consider the patterns of distribution seen among living angiosperms in the light of these deductions.

REVIEW OF EXISTING GROUPS

We have had no opportunity to investigate the great majority of angiosperm orders in detail, but offer the following comments, arranged according to the system of Thorne (1968), to illustrate the major patterns that do exist in the group. In the following notes, we have used especially *Die Natürlichen Pflanzenfamilien* (Engler & Prantl, 1887–1915) and *Das Pflanzenreich* (Engler, 1900–1953), Airy Shaw (1966), and Hutchinson (1959). The following more local works have also been very useful: Burbidge (1963), Standley (1920–1926), Muñoz Pizarro (1966), Thorne (1965), Guillaumin *et al.* (1965), and Hillebrand (1888).

No extensive effort has been made to review the paleobotanical literature, especially since the identification of Cretaceous and Paleogene angiosperms with modern forms presents so many difficult problems. We do, however, mention a few records when they appear to be of special interest in relation to the distribution of patterns being discussed. In this connection, the bibliography assembled

by Graham (1973*b*) has been especially helpful. In the following pages, the orders of dicots are presented first, in alphabetical order, followed by the orders of monocots.

DICOTYLEDONEAE

Annonales.—Illiciaceae, Schizandraceae, Magnoliaceae, Calycanthaceae, and Saururaceae seem clearly to be Laurasian families, originating in the Northern Hemisphere and in some cases spreading southward subsequently. This implies a Miocene or more recent dispersal of Magnoliaceae from North into South America (Lozano Contreras, 1972), where *Talauma* and *Magnolia* are the only genera. Magnoliaceae have seeds with sarcotestas, which are eaten by birds, and the seeds are easily dispersed. Aristolochiaceae likewise appear to be Laurasian, but the *Aristolochia* line is well represented in South America, where many species of *Aristolochia* as well as the related endemic genera *Holostylis* and *Euglypha*, occur. Relatively early sweepstakes dispersal from North America probably accounts for this. Judging from the distribution of their possibly more primitive relatives, Saururaceae, the pantropical Piperaceae may also have had a Laurasian origin, perhaps reaching South America *via* Africa. Piperaceae are reported from the Eocene of Argentina (Menéndez, 1972).

A number of families of Annonales are common to Africa and South America, with most also extending to tropical Asia. Especially in view of their antiquity, it seems probable that some of them migrated more or less directly between South America and Africa when they were in closer contact. These families include Canellaceae (well represented in West Indies), Myristicaceae, Siparunaceae, and Annonaceae. On the other hand, Gyrocarpaceae and Hernandiaceae, easily dispersed judging from present distributions, may not be so ancient, although their modern distributions link Africa and South America.

Annonaceae, which evidently did migrate directly between Africa and South America (Smith, 1973), apparently radiated extensively in tropical Asia by Paleogene time. Indeed, they radiated to such an extent that Takhtajan (1969) was misled into considering the family primarily disjunct between Asia and South America. The incisive studies of Walker (1971, 1972) have clearly shown this family to have a West Gondwanaland distribution. The two temperate North American genera, *Asimina* and *Deeringothamnus*, are more closely related to African genera such as *Hexalobus* and *Uvariastrum* than to any South American genus. Their ancestors doubtless reached North America from Africa *via* Europe by Early Eocene time or earlier. All other genera of Annonaceae found north of Panama are probably Neogene or more recent arrivals from South America. Annonaceae are well represented in the Eocene of southern England (Chandler, 1964) and reported from the Eocene of Argentina (Menéndez, 1972), as well as from the Paleocene of Egypt (Chandler, 1954) and Colombia (Hammen & García de Mutís, 1966).

Judging from the complex interrelationships of American and Old World genera, Monimiaceae s. str. seem to have spread directly between Africa (where four genera, three endemic, and about 40 species occur on Madagascar and the Mascarenes, but none at the present day on the mainland) and South America, and

seem to have evolved early enough to have reached Australasia more or less directly. Monimiaceae are known from the Senonian of Europe (Rüffle, 1965), and reported from the Upper Cretaceous of Argentina (Menéndez, 1972).

Lauraceae, much more poorly represented in Africa than in South America or tropical Asia at present, presumably also dispersed directly between South America and Africa. The family is reported from the Upper Cretaceous of Argentina (Menéndez, 1972). *Ocotea* has hundreds of species in tropical America and a few in Africa; *Beilschmeidia* also occurs on both continents. Much extinction took place among the Lauraceae of Africa, as judged from the contemporary occurrence of four genera in the Canary Islands. One of these, *Persea* (Kopp, 1966), consists of two subgenera in the Western Hemisphere, of which subg. *Persea* seems to be North American, subg. *Eriodaphne* South American. *Persea* is known in North America from at least Eocene times onward (MacGinitie, 1941), and wood very similar to that of this genus is known from the Eocene of Patagonia (Romero, 1970). *Persea* (with *Machilus*, *Nothophoebe*, and *Alseodaphne*; Kostermans, 1952), is an old Laurasian genus, but subg. *Eriodaphne* evidently was South American and may have spread north of Panama only in the Miocene or more recently, where it came in contact with subg. *Persea*. Although *Persea* is not now found on the mainland of Africa, it thrives on the Canary Islands, and it seems reasonable to assume that the ancestors of subg. *Eriodaphne* reached South America *via* Africa more or less directly by Paleocene time. *Umbellularia* and *Sassafras* (the latter included in *Persea* by Kostermans, 1964) are ancient offshoots of the *Persea* line which survive with restricted ranges in North America, and, in the case of *Sassafras*, in Asia also. *Litsea* and *Lindera* are Laurasian genera represented today by a few species in the North American region. All other American genera of Lauraceae seem to have reached Central and North America and the West Indies from South America, commencing in Paleogene time, and with fossils of leaves very similar to those of *Ocotea*, *Nectandra*, and *Beilschmeidia* in North America by the Middle Eocene (MacGinitie, 1969; Dilcher, 1973*b*).

Drimys, the sole representative of Winteraceae in South America, may have dispersed from Australasia to South America *via* an Antarctic route prior to the full separation of Australia from Antarctica (Raven & Axelrod, 1972). Direct connections have been overemphasized, however, by the lumping of *Drimys* with the Australasian genus known as *Tasmannia*. Whereas *Tasmannia* has a gametic chromosome number $n = 13$, *Drimys*, like other genera of Winteraceae that have been studied, has $n = 43$ (Raven & Kyhos, 1965; Ehrendorfer *et al.*, 1968). Since a species of the otherwise Australasian genus *Bubbia* occurs in Madagascar, an alternative hypothesis is that *Drimys* was derived from a West Gondwanaland stock of Winteraceae which subsequently became extinct on the mainland of Africa. The single species of *Bubbia* in Madagascar should be compared with *Drimys*. As L. J. Hickey (personal communication) has pointed out, however, the pollen of Winteraceae is specialized within Annonales, and the fossil record of the family begins in the Early Oligocene. In view of this, the simplest assumption would be that the Antarctic dispersal route for Winteraceae to the New World is correct, and that the species of *Bubbia* on Madagascar reached it from

the east by long-distance dispersal. Its fruits are fleshy and perhaps it is readily dispersed.

Chloranthaceae are known from four genera: *Hedyosmum*, which has about 40 species in tropical America and the West Indies and one in Hainan(!); *Ascarina*, with 8 species in Malaysia, Polynesia, and New Zealand; *Ascarinopsis*, one species, Madagascar, related to *Ascarina*; and *Chloranthus*, with about 15 species in East Asia and Indomalaysia. The family appears to be Laurasian in origin, and it is logical to presume that the ancestors of *Ascarinopsis* reached Madagascar by long-distance dispersal from the east. *Hedyosmum* may have differentiated in tropical Laurasia and spread to North America and then to South America perhaps in later Neogene time.

Other families of Annonales are more restricted in distribution, either to Australasia—Degeneriaceae, Eupomatiaceae, Himantandraceae, Austrobaileyaceae, Amborellaceae, Trimeniaceae, Idiospermaceae (Blake, 1972)—or to South America—Lactoridaceae, Gomortegaceae—or to both—Atherospermataceae (Schodde, 1970). Another restricted group, probably deserving recognition as a distinct family, is the Monimiaceae—Hortonioidae of Ceylon. It probably was derived from West Gondwanaland stock, and may have survived during the passage of India northward to Asia (= “Noah’s ark” distribution; Axelrod, 1971, 1972c; McKenna, 1973). We know of only one other vascular plant—*Schumacheria* (Dilleniaceae)—that we think might have survived in India during its northward passage from Africa, but Schuster (1972) has proposed that several genera of liverworts may have been transported to Eurasia in this manner. For Winteraceae, Chloranthaceae, and the common ancestors of Thorne’s (1968) suborders Magnoliineae (Magnoliaceae, Degeneriaceae, Eupomatiaceae, Himantandraceae) and Laurineae (Austrobaileyaceae, Chloranthaceae, Amborellaceae, Trimeniaceae, Monimiaceae, Atherospermataceae, Siparunaceae, Calycanthaceae, Lactoridaceae, Gomortegaceae, Lauraceae, Hernandiaceae, Gyrocarpaceae, Idiospermaceae) a warm-temperate or tropical route from West Gondwanaland to Australasia seems probable, as it does for Monimiaceae s. str. Atherospermataceae may have originated in the more temperate latitudes of Australasia, reaching South America secondarily *via* Antarctica.

Asterales.—No fossil pollen of the vast family Asteraceae is known prior to the uppermost Oligocene, despite extensive search (Germeraad *et al.*, 1968; Leopold, 1969; Becker, 1969; Muller, 1970), and pre-Miocene records are exceedingly few. The Cretaceous *Palaeanthus* (Newberry, 1896) is probably a cycadophyte and certainly not a composite (T. Delevoryas, personal communication; A. Cronquist, personal communication). No Asteraceae have what appears to be a distribution achieved by direct migration between Australia and southern South America, suggesting with other evidence no more than a mid-Oligocene age for the family. The migrations of Asteraceae, consisting of many very readily dispersed genera, must therefore be seen in the light of present geography. Primitive Heliantheae and Mutisieae, the most generalized tribes, are concentrated in northern South America, which may be a likely place of origin for the family. Considering that the family is in the Lower Miocene in New Zealand (Couper, 1960), northern South America, Nigeria, and eastern Asia, and rapidly increases

in abundance in all areas (Germeraad *et al.*, 1968), and that the tribe Cichorieae appears in the Upper Miocene in nearly all areas that have been sampled, dispersal must have been extremely rapid (Raven, 1973*b*). Asteraceae have rapidly produced many genera and species in response to the worldwide expansion of semiarid and subhumid habitats in Neogene time and subsequently. If Calyceraceae are closely related to Asterales, this provides additional evidence suggestive of a South American origin for Asteraceae, but might not accord with a postulated derivation for both from Dipsacales.

Balanopales.—The affinities of the single family Balanopaceae, which is confined to the warmer portions of Australasia, are obscure (Wolfe, 1974; R. F. Thorne, personal communication). Its ancestors may have reached this region in mid-Cretaceous time, or earlier.

Batidales.—The single genus is widespread along warm shores.

Berberidales.—Menispermaceae seem to have a West Gondwanaland pattern at the present day, but if *Pycnarrhena*, an Asian genus of about 25 species of which one reaches Australia, is primitive, the origins of the family could be Laurasian, as suggested by J. A. Wolfe (personal communication). The family is in the Eocene of Europe (Chandler, 1964) and the Early Oligocene of Oregon (Scott, 1954). The other families of the order are without doubt Laurasian, with Sargentodoxaceae, Ranunculaceae, Berberidaceae, and Papaveraceae either restricted there or represented by only scattered species in the Southern Hemisphere that are closely related to northern relatives. The major puzzle in the distribution of Berberidales is the presence of two endemic genera (*Boquila* and *Lardizabala*) of the chiefly East Asian Lardizabalaceae in Chile. Perhaps Lardizabalaceae were in Africa in the Cretaceous, for their present distribution is truly relict; otherwise a very early and unlikely long-distance dispersal to South America, followed by extinction in North America, must be postulated. The order certainly seems to have originated in Laurasia.

Bignoniales.—Bignoniaceae, better represented in South America than in Africa or Asia, seem to have existed when more direct migration between Africa and South America was possible, judging from their present distribution. Although *Neosepidacea* is endemic to New Guinea and Queensland, Bignoniaceae are very poorly represented in Australasia, where they may not have arrived prior to the Miocene. Most of the North American representatives of the family have probably come from South America except *Catalpa*, *Campsis*, and possibly *Chilopsis*. Crescentieae consist of 3 or 4 genera of Central America; the 9 genera endemic to Madagascar with *Kigelia*, endemic to continental Africa, seem to have been derived independently from Tecomeae (A. Gentry, personal communication). The herbaceous genera *Argylia* (Andes) and *Incarvillea* (Asia) are closely related but anomalous in the family; their distribution recalls that of Lardizabalaceae.

Pedaliaceae are primarily African, with some representation, including the endemic *Trapella*, in tropical Asia and one species of *Josephina* reaching Australia. Martyniaceae, on the other hand, are South American, with the monotypic *Martynia* endemic to Mexico. Myoporaceae appear to be primarily Australasian, though the monotypic *Bontia* is West Indian, and *Leucophyllum*, currently re-

ferred to Scrophulariaceae, is North American (S. Tomb, personal communication). The African *Oftia* is discordant in the family (Takhtajan, 1969; S. Tomb, personal communication), and better referred to Scrophulariaceae (Dahlgren & Rao, 1971). The West African *Zombiana*, mentioned by Dahlgren and Rao (1971) as an obscure genus of Myoporaceae, is in fact a synonym of *Rotula* (Boraginaceae; Heine, 1963). Myoporaceae presumably achieved their disjunct distribution by Paleogene trans-Pacific dispersal.

Scrophulariaceae are Laurasian, with well developed elements in Africa. Despite a proliferation of species in some genera in Australasia (the *Veronica*-complex) and in South America (*Calceolaria*, *Jovellana*, *Angelonia*, a few other small endemic genera), the family, which consists of many readily dispersed plants, a number of them of moist habitats, appears to be a fairly recent arrival in both areas. Scrophulariaceae were not represented, as far as known, in the Paleogene of England (Chandler, 1964). Some genera, such as *Lamoureauxia* (Ernst, 1972), apparently originated in tropical North America and subsequently spread to South America. There are no evident connections between the Scrophulariaceae of Africa and those of South America, except in widespread weedy genera, implying that the family may not have been in existence when these continents were in closer proximity.

Plantaginaceae are presumably basically Laurasian and are widespread, but an endemic monotypic genus, *Bougueria*, is in the Andes. Orobanchaceae are likewise Laurasian, although *Orobanche* has attained a nearly cosmopolitan distribution. Lentibulariaceae are extremely widespread herbs of wet places for which it is not possible at present to postulate a place of origin.

The pollen of Acanthaceae is, curiously, not known from the fossil record until Neogene time (Muller, 1970), although fruits from the Eocene of England are referred to *Acanthus* (Chandler, 1964). Judging from the distribution of some genera, Acanthaceae must often be easily dispersed, even though they are very poorly represented in Polynesia and not known as native plants in the Hawaiian Islands. Despite the existence of very few small endemic genera, Acanthaceae definitely seem to be newcomers in Australasia. The family is well represented in Africa (including Madagascar), South America, and tropical Asia, suggesting some antiquity. Their pollen appears in the first two of these areas in the Miocene but in Asia not until the Mio-Pliocene (Germeraad *et al.*, 1968). Some groups, such as the Thunbergioideae, are confined to the Old World; others, such as *Mendoncia* and *Justicia*, are common to Africa and South America. The curious genus *Oplonia* (Stearn, 1971) is common to tropical America and Madagascar. Moderately large genera such as *Carlownrightia* in North America seem to provide evidence of an early Laurasian element.

Gesneriaceae consist of two subfamilies. The African and Eurasian, mainly tropical Asian, Cyrtandroideae include some genera that reached Australasia (*Boea*, *Didymocarpus*) and one which is in Australia and the Pacific Islands (*Cyrtandra*). The principally South American Gesnerioideae include the small genera *Coronanthera*, *Rhabdothamnus*, and *Fieldia*, which are Australasian. *Rhabdothamnus* and probably also *Coronanthera* are very distinctive within the

family in terms of their flavonoids (Lowry, 1973), possibly suggesting a relict status and not a direct derivation from South American forms, at least in recent time. *Fieldia* is not closely related to the other two genera but allied to a group of small Chilean genera. Its Paleogene ancestors probably entered Australasia by a cool-temperate path across Antarctica. Gesneriaceae were probably in existence when Africa and South America were in closer contact, while the major groups of the family differentiated subsequently.

Summarizing, Bignoniales seem to have originated when Africa and South America were closer, perhaps in early Paleogene time. The same may be said for the ancestors of Myoporaceae, Bignoniaceae and Gesneriaceae, whereas the other families, including Scrophulariaceae, Pedaliaceae, and Martyniaceae, may have appeared subsequent to the wider separation of Africa and South America. Myoporaceae can be compared with the most primitive elements in Scrophulariaceae, and these two families probably had a common ancestor early in the differentiation of Bignoniales.

Campanulales.—Campanulaceae are widely distributed and evidently easily dispersed. The geography of the family suggests a Paleogene age, as exemplified by Cyphioideae in Africa and South America. In general, Campanuloideae appear to be a Laurasian–African group, Lobelioideae southern. Pentaphragmataceae are tropical Asian, Goodeniaceae are essentially Australasian and perhaps not directly related to Campanulaceae (Carolin, 1960; Raven, 1975).

Capparales.—Capparaceae have a West Gondwanaland–tropical Asian distribution, and are known from the Eocene of southern England (Chandler, 1964). If *Oceanopapaver* of New Caledonia is correctly assigned here (Thorne, 1968: 60), when and how it reached Australia is problematical. It is the only strongly distinctive endemic member of the entire superorder Cistiflorae in Australasia. Moringaceae, with a single genus and about a dozen species, are mainly African but extend to India. Resedaceae are mainly North African and Mediterranean and extend eastward to Central Asia and India; they presumably reached South Africa by long-distance dispersal. The family seems to be introduced in the Western Hemisphere, judging from the relationships of the species (Abdallah, 1967; Raven, 1971). Brassicaceae are cosmopolitan in temperate regions, and occur in New Zealand by Oligocene time (Raven, 1973*b*). They appear to be a Laurasian group, but are well represented in South America. Unusual genera are scattered throughout the world, and members of the family are apparently easily dispersed. Whether the order originated in West Gondwanaland or Laurasia is problematical, but the pattern for the whole Cistiflorae suggests the former.

Casuarinales.—The single family is Australasian and known from the Tertiary of South America. It presumably crossed Wallace's line in Neogene time (Raven & Axelrod, 1972). It is one of the few "Amentiferae" in the Southern Hemisphere, and is known from Middle Eocene fossils in Australia (Lange, 1970) and Miocene ones in Argentina (Frenguelli, 1943). Maastrichtian pollen records (Couper, 1960; Raven & Axelrod, 1972) from New Zealand are not definitively assignable to this genus (Mildenhall & Harris, 1971; Wolfe, 1974). The evidence for a relationship with Hamamelidales seems convincing.

Chenopodiales.—Although the pattern has been obscured by the ready dispersal mechanisms of some families, it is clear that the *Chenopodiales* (*Centrospermae*) differentiated in West Gondwanaland when Africa and South America were in closer contact (Turner, 1973). *Caryophyllaceae* have an essentially Laurasian distribution, although they have spread repeatedly into different southern continents. All of the other families are basically southern. Fossil pollen of *Caryophyllaceae* first appears in the Oligocene (Muller, 1970), although *Hantsia*, from the Eocene of southern England, has been assigned to this family (Chandler, 1964).

Phytolaccaceae may have been in existence when Africa and South America were in more or less direct contact, judging from the existence of the endemic South African *Lophiocarpus*; other families appear to have been more recent in origin. Other primarily South American families are *Nyctaginaceae*, *Cactaceae* (the North American *Cactaceae* must be derived, Buxbaum, 1969, and there is no fossil record; Brown, 1959), *Portulacaceae*, *Halophytaceae*, and perhaps *Polygonaceae*, reported from the Upper Cretaceous of Argentina (Menéndez, 1972), and extremely well developed in Laurasia. *Basellaceae* consist of five genera, of which only *Basella* is found in the Old World, with two species in tropical Africa and three in Madagascar. This pattern suggests an origin in South America followed by long-distance dispersal to Africa. Basically African families are *Aizoaceae* and *Didiereaceae* (Madagascar).

Chenopodiaceae and *Amaranthaceae* are now so widespread in semiarid regions it is difficult to suggest the area of their early evolution. The Australian family *Gyrostemonaceae*, consisting of five genera and about 15 species of trees, shrubs, and herbs, many in temperate areas, probably is derived from *phytolaccaceous* ancestors that reached Australia *via* Antarctica and a cool temperate route. Other *Chenopodiales* appear to be relatively recent arrivals in Australia, where *Polygonaceae* probably arrived partly by this southern route (*Muehlenbeckia*), partly from the north, and other groups probably appeared in Oligocene time or more recently by relatively long-distance dispersal, radiating in the expanding desert and semiarid regions there (Raven & Axelrod, 1972).

In summary, the common ancestor of *Chenopodiales* seems to have been present, possibly with ancestral *Phytolaccaceae*, when Africa and South America were still in relatively close proximity—perhaps in early Paleogene time. The *phytolaccaceous* ancestors of *Gyrostemonaceae* must have reached Australia early, just as the ancestors of *Stegnosperma* must have reached North America early. Most families of the group differentiated in South America, Africa, and Laurasia (*Caryophyllaceae*), after these areas were well separated. This agrees with Muller's (1970: 438) suggestion that *Chenopodiales* commenced their main differentiation by Paleocene-Eocene time. A rather distinctive pollen of this order marks the basal Paleocene in the Atlantic Coastal Plain (J. A. Wolfe, personal communication).

Cistales.—*Flacourtiaceae* have a West Gondwanaland-tropical Asian distribution (to southern England in the Eocene, including the tropical African *Oncoba*; Chandler, 1964), are evident newcomers in Australasia, and may have reached Central and North America only in Neogene time. *Cochlospermum* (*Cochlo-*

spermaceae) has a similar distribution. The second genus, *Amoreuxia*, is presumably basically South American, and probably entered Central and North America in Neogene time. Dipentodontaceae and Scyphostegiaceae are tropical Asian, Peridiscaceae Brazilian, Bixaceae basically South American, Malesherbiaceae western South American, and Achariaceae South African. Violaceae are readily dispersed, but many center in South America and Laurasia, with some species of *Rinorea* and *Hybanthus* in Africa and Asia. The monotypic *Decorsella* is West African, whereas *Melicytus* and *Hymenanthera* are Australasian, as is *Agatea*. Perhaps Violaceae differentiated in South America after its separation from Africa and spread widely subsequently. *Viola* is especially widespread.

Cistaceae are Laurasian, with the ancestors of *Crocanthemum* presumably having reached South America in the Miocene or more recently. Datisceae are also clearly Laurasian. Turneraceae have an African–South American distribution, with some genera having reached Central and North America in Neogene time or more recently. Caricaceae are similar in their pattern of distribution, but the endemic genus *Jarilla* may have a relatively great antiquity in Mexico, where its ancestors probably arrived from South America. Begoniaceae are also similar, but evidently easily dispersed in tropical and subtropical regions.

Passifloraceae are chiefly African, with some genera represented in tropical Asia and a few species even reaching Australasia, where they are clearly recent arrivals (Wilde, 1972). The large genus *Passiflora* is mainly American, and three other genera exclusively so. Cucurbitaceae (Jeffrey, 1962) are well represented in South America, Africa, and tropical Asia, implying antiquity. They have also reached Australia, where there is a moderate representation of genera. Temperate North American and Eurasian genera probably are derived from Laurasian ancestors, such as those represented in the Paleogene of southern England (Chandler, 1964). The North American Paleocene *Vitis lobata* (Knowlton) Brown (1962) is clearly Cucurbitaceae (J. A. Wolfe, personal communication). Loasaceae are best represented in South America. However, *Kissenia* is in South-West Africa and near the mouth of the Red Sea, and several genera, some endemic, are in Central and North America. The family probably dispersed between South America and Africa when these continents were closer. Judging from its diversity, it may have reached North America in Early Miocene time, or earlier.

To summarize for Cistales, the primary differentiation of the families seems to have taken place in West Gondwanaland in Upper Cretaceous time. There are a number of taxa common to Africa and South America, with a number of small, endemic families on each of these continents and a few in tropical Asia. Datisceae and Cistaceae are primarily Laurasian, with wood of the former reported from the Eocene of India (Lakhanpal, 1970). Their ancestors presumably reached Eurasia from Africa in Paleogene time. Cistales are mainly represented in Australasia by widespread taxa.

Cornales.—Rhizophoraceae have their greatest diversity in the Old World tropics. Of the non-mangrove genera, *Cassipourea* occurs in South America, Africa, Madagascar, and Ceylon, and one species of the mainly African and Asian *Anisophyllea* is in South America—implying a West Gondwanaland history.

The tribe Rhizophoreae itself, abundantly represented by fossil pollen, had originated by the Eocene, possibly in Southeast Asia, and then spread to tropical America (in the Eocene) and Africa (Germeraad *et al.*, 1968: 281–2). *Bruguiera* is reported from the Eocene and Oligocene of England (Chandler, 1964).

Vitaceae are mainly Laurasian and African, with a few widespread tropical genera in South America. Despite the endemic monotypic *Clematocissus*, they do not appear to be of great antiquity in Australasia. Vitaceae are reported from the Eocene of India (Lakhanpal, 1970). Nyssaceae are Laurasian, Garryaceae North American. Alangiaceae consist only of the African and tropical Asian *Alangium* (which reaches Australia). *Alangium* was widespread in the Tertiary throughout Laurasia (Eyde, 1972*b*). The South American *Metteniusia* should not be referred to Alangiaceae (Eyde, 1968, contrary to Hutchinson, 1959). *Alangium* probably does not belong to Cornales (Eyde, 1968). Cornaceae are chiefly Laurasian, with the monotypic *Afrocrainia* in East Tropical Africa; all other non-Laurasian genera referred to the family may belong to other groups (Thorne, 1973*b*). The subfamily Mastixioideae was richly represented in the Paleogene of Europe (Chandler, 1964) and western North America (Scott, 1954; in Chandler, 1964: 58; MacGinitie, 1969: 129). *Griselinia* of South America and New Zealand probably does not belong to Cornales and might be closer to Escalloniaceae (= Saxifragaceae sens. lat.; Philipson, 1967). *Corokia*, of New Zealand and Polynesia, is referred by Airy Shaw (1966: 285) and by Eyde (1966) to the Escalloniaceae also, where it is certainly more at home on phytogeographic grounds. Haloragaceae are cosmopolitan, centering in Australia in terms of diversity. *Gunnera* (Gunneraceae; Thorne, 1973*b*), easily dispersed in view of its occurrence on the Hawaiian Islands, seems at present also to be southern, but its pollen is reported from the Maastrichtian of the western United States (Lef-fingwell, 1966; Chmura, 1973). Hippuridaceae are circumboreal waterplants, also found in southern South America.

In the suborder Araliineae, Araliaceae are evidently easily dispersed and well represented on islands, including the Hawaiian Islands. The family is reported from New Zealand in the Lower Eocene (Couper, 1960). There are several endemic genera in Australasia and also in Polynesia (*e.g.* *Pterotropia*, *Cheiro-dendron*). Araliaceae are well represented in Laurasia, especially tropical Asia. They are more diverse in South America than in Africa. *Dendropanax* has been reported from a number of localities in Laurasia in the early Tertiary (Dilcher & Dolph, 1970; Dilcher, 1973*b*; Leopold & MacGinitie, 1972). Araliaceae had reached Australasia by the mid-Eocene (Couper, 1960), possibly by a combination of long-distance dispersal and migration across India-Antarctica in the Late Cretaceous or Early Tertiary. Araliaceae seem almost certainly to have been in existence when more or less direct migration between South America and Africa was possible, and, if it is correctly placed here (Airy Shaw, 1966), the New Caledonian *Phelline* also might be derived from ancestors that reached Australasia very early.

In the Apiaceae, Hydrocotyloideae definitely have a West Gondwanaland distribution (*e.g.* Mathias & Constance, 1965). Saniculoideae and Apioideae (possibly with the exception of *Oreomyrrhis*; Raven, 1973*b*) are chiefly Laurasian

but have a strong representation in Africa, probably mostly achieved since the Miocene, and a lesser one in South America. The numerous South American species of *Eryngium* may have been derived from tropical North American ancestors in Neogene time and more recently. In Australasia, where they are probably recent arrivals (Raven, 1973b), Apiaceae have evolved rapidly to produce a series of distinctive taxa.

Summarizing for Cornales, Rhizophoraceae, Araliaceae s. str., and Apiaceae-Hydrocotyloideae seem to have been in Africa and South America when these continents were closer together, whereas Cornaceae and Vitaceae, also relatively ancient families, might have been more or less confined to Laurasia at that time and reached the Southern Hemisphere subsequently.

Dipsacales.—Caprifoliaceae are Laurasian, with recent incursions into the southern continents, including that of *Sambucus* to Australia. The monotypic Adoxaceae are also Laurasian. Valerianaceae are Laurasian, but they have proliferated in South America, where they are probably not very old. Dipsacaceae are Eurasian, Calyceraceae South American. In general, the order is Laurasian, very poorly developed in Africa, and virtually absent in Australasia. If Calyceraceae belong with this order, their ancestors may have reached South America *via* Africa, where the order is poorly represented, or by early long-distance dispersal from North America. Since such a great age for the family appears unlikely, they might better be associated with Asterales, as is traditional. Takhtajan (1969) has placed them in a separate order, next to Asterales.

Ebenales.—Ebenaceae are perhaps basically an African family, with *Diospyros* having reached Laurasia presumably by Paleocene time at the latest (Chandler, 1964) and migrating throughout Eurasia and North America. Since the North and South American species of *Diospyros* are related respectively to Eurasian and African groups, not to one another, a Cretaceous West Gondwanaland history is implied. *Oncotheca* of New Caledonia, sometimes considered to be ebenaceous, may better be referred to Theales (Takhtajan, 1969). *Diospyros* is common to Africa and South America, with a few species related to Asian ones also in Australasia.

Sapotaceae, with about 128 genera, are viewed by Aubréville (1973) as consisting of 17 groups, six of Laurasian and eleven of Gondwanaland distributions. They are known from the Eocene of Europe (Chandler, 1964; Krutzsch, 1967) and from the Oligocene of the eastern United States (Traverse, 1955). An origin in West Gondwanaland appears most probable, almost certainly before the close of the Cretaceous; both the *Manilkara* group and the pentasepalous group are common to Africa and South America. The Australian species appear to have been derived in the Neogene or more recently from tropical Asia, although *Amorphospermum* (1 sp.) and *Niemeyera* (2 sp.) are endemic genera of tropical Australia related to *Chrysophyllum*. The relationships of the genera on New Caledonia and other Pacific Islands are probably ultimately with those of tropical Asia. Exchange between Africa and tropical Asia evidently took place in or before the Paleocene, and plants of this family appear to have been relatively well dispersed since.

Symplocaceae evidently have a Laurasian distribution, probably having en-

tered Australasia (including New Caledonia) in the Miocene or subsequently. The family is absent from Africa, but well represented in South America. The South American species of *Symplocos* may be derived from a complex that existed in tropical North America prior to the linking of North and South America. However, the genus might be older and thus have reached South America *via* Africa. Styracaceae are best represented in Asia but with *Styrax* in North America in the Eocene and secondarily reaching South America, presumably in the Neogene. The affinities of the Brazilian *Pamphila* should be investigated in the context of the family before drawing definite conclusions about its paleobiogeography. *Afrostryax* of West Tropical Africa has been placed with *Hua* in Huaceae and considered of sterculiaceous affinity (Chevalier, 1947; Airy Shaw, 1966: xxi; Takhtajan, 1969), but other authors such as Hutchinson (1959) and Hepper (1963, and personal communication) retain it in Styracaceae. Lissocarpaceae are tropical South American.

To summarize, Sapotaceae and Ebenaceae seem to have a West Gondwanaland distribution, while Symplocaceae are apparently Laurasian. On the balance, the order may have originated in West Gondwanaland.

Ericales.—Ericaceae seem to have a Laurasian-West Gondwanaland distribution (*e.g.* Stevens, 1970). The common ancestor of *Gaultheria* and *Pernettya* probably arrived in southern South America relatively early, by long-distance dispersal, and then spread from there, as did *Acaena*. Empetraceae, like *Gaultheria-Pernettya*, are probably Laurasian and recent arrivals in the Southern Hemisphere. Epacridaceae, judging from their diversity, seem to be a group of some antiquity in Australasia; the earliest fossil record, however, is from the Upper Eocene (Couper, 1960). The bipolar dichotomy between Ericaceae and Epacridaceae may represent divergence from a tropical alliance of West Gondwanaland. Epacridaceae, including the tribe Styphelieae, are reported from the Early Eocene of southern England (Chandler, 1964), but these records should be reexamined critically in the context of the living members of the family.

Euphorbiales.—Euphorbiaceae are extremely widespread and easily dispersed. They are mainly tropical in distribution, and may have been common to Africa and South America when these continents were much closer. A number of genera, a few of them endemic, occur in Australasia, and *Poranthera* and *Ricinocarpus* are especially distinctive (Airy Shaw, 1966). The oldest known fossils of Euphorbiaceae are Paleocene (Chandler, 1954; Muller, 1970). The occurrence of the related families Aextoxicaceae in Chile, Pandaceae in West Tropical Africa, and Didymelaceae in Madagascar makes the origin of Euphorbiaceae in West Gondwanaland seem likely. Koch (1972) compared fruits from the latest Cretaceous of Greenland with those of the West Indian *Picrodendron*, often considered a distinct family but grouped by Thorne (1968) with Euphorbiaceae; however, Koch (personal communication) has subsequently withdrawn his suggestion of affinity. Dichapetalaceae, with two endemic genera in tropical South America, one on Madagascar, one (*Tapura*) common to South America and Africa, and a fifth (*Dichapetalum*) found in all three main tropical regions of the world, were almost certainly present in Paleogene time when Africa and South America were much closer.

Buxaceae are an ancient group, with *Sarcococca* Asian, *Pachysandra* Laurasian, *Buxus* Laurasian and ranging also into tropical and southern Africa and Madagascar (including *Notobuxus*). *Pachysandra* or *Sarcococca* is known from fossil pollen in the Maastrichtian. *Styloceras* of South America has traditionally been grouped with the African *Notobuxus* in a tribe Stylocereae, but Airy Shaw (1966) separated it as a distinct although related family. Buxae are clearly Laurasian, but the group also seems to have been in West Gondwanaland when more or less direct migration between South America and Africa was possible. *Simmondsia*, a genus of uncertain affinity and probably autochthonous in the southwestern United States and adjacent Mexico, appears best referred to a monotypic family Simmondsiaceae (Airy Shaw, 1966: 1040). Thymelaeaceae are best represented in Africa but have some antiquity in Laurasia (cf. *Dirca*, *Daphne*, *Thymelaea*, *Aquilaria*, *Lagetta*: also in the Eocene of southern England; Chandler, 1964) and in Australia, where three endemic genera (*Phaleria*, *Pimelea*, *Drapetes*) occur. The family is certainly older than the present Oligocene limit of its fossil occurrence (Muller, 1970). Such genera as *Lophostoma*, *Lasiadenia*, and *Daphnopsis* are basically South American.

Summing up for Euphorbiales, the group has considerable antiquity both in West Gondwanaland and in Laurasia, and a temperate element evolved very early. The rich representation of Thymelaeaceae in Australasia, South America, and Africa suggests differentiation of the order by the Upper Cretaceous.

Fagales.—The Fagaceae are primarily Laurasian, and the genus *Quercus* has spread to South America probably in the Pliocene or more recently. How *Nothofagus* reached the Southern Hemisphere is unknown (Raven & Axelrod, 1972), but it is represented by abundant pollen in the Maastrichtian of Australia, New Zealand, and southern South America. In Africa, *Quercus* occurs today in the Atlas Mountains and adjacent areas, a region which it had already reached in the early Quaternary. Post-Eocene woods of Fagaceae (derived from sites in the Anti-Atlas?) are recorded near Tindouf in Spanish Morocco (*in* Aubréville, 1970). The absence of Fagaceae in the high mountains of north-central Africa (Hoggar, Tibetsi) today may be explained by expanding dry climate which eliminated earlier forests from the region. Furthermore, montane pathways comparable to the American Cordillera do not now provide a route into lower latitudes. There are no reliable records of Cretaceous or Paleogene Fagaceae either in India (see Lakhanpal, 1970: 685) or in Africa south of the Mediterranean region. The pollen record of *Nothofagus* and other now austral genera reported from the Cretaceous of Nigeria (Puri, 1965) is based on a sample of drilling mud carried in from another region (Prof. A. T. Cross, written communication, Sept. 1972), and hence is not valid. Pollen of *Nothofagus* about 10,000 years BP in sediments in the Cape Flats of South Africa is thought to have been blown from South America (Schalke, 1973). A mid-Cretaceous migration of an ancestral group from southern (montane) Eurasia into Australasia *via* Africa-India seems required to account for the presence of *Nothofagus* in austral regions. At that time ancient highs on the Precambrian basement terrain, now largely reduced by erosion, may have afforded a route for entry into the temperate Southern Hemisphere. The existence of the distinctive *Nothofagus* by Maastrichtian time suggests an origin

for the family at least by early Senonian time or earlier—pending a review of Turonian and Cenomanian fossils that have been referred here.

Betulaceae are Laurasian, and *Alnus* has reached South America in the late Miocene or more recently. Wood of the tribe Coryleae occurs in the latest Campanian (~ 72 m.y. BP) of California (Page, 1970), with pollen of *Alnus* known from the Maastrichtian onward (Wolfe, 1974).

Gentianales.—Of the three subfamilies of Loganiaceae (Thorne, 1968), Buddleioideae are mainly African, the genus *Buddleia* itself widespread in Laurasia, with its arrival in South America probably Neogene. Desfontainioideae have *Anthocleista* in Africa and Madagascar, *Desfontainia* and *Potalia* in South America, and *Fagraea* in tropical Asia, extending to Polynesia and Australia—clearly a West Gondwanaland nuclear group. Loganioidae are mainly African and Laurasian, but one species of the African *Mostuea* occurs in Brazil. The genus *Logania*, with about 25 species, is Australasian, and *Labordia*, with about 25 species also, is endemic to Hawaii. The general distribution indicates that at least some Loganiaceae are relatively easily dispersed, and we therefore assume that *Logania* is not necessarily ancient in Australasia.

Among related groups segregated as families by Hutchinson (1959), Antoniaceae have three genera in South America, one in Malaysia, and the monotypic *Usteria* in West Tropical Africa, again a West Gondwanaland pattern. The herbaceous Spigeliaceae are widespread in tropical regions and may be relatively easily dispersed. Strychnaceae are tropical Asian, but *Scyphostychnos* is tropical African and *Strychnos* African, South American, and tropical Asian, just entering Australasia. The loganiaceous complex as a whole, and the elements called Desfontainioideae, Antoniaceae, and Strychnaceae, probably existed when more direct dispersal was possible between Africa and South America; this may have been the case for the genus *Strychnos* also. In spite of the endemic *Logania*, the family (sens. lat.) is apparently represented mainly by recent arrivals in Australasia and Polynesia.

The huge, widespread family Rubiaceae (Verdcourt, 1958), despite the presence of at least three small endemic genera in Australia and a good representation in Australia, New Caledonia, and even Hawaii, seems to consist mainly of recent arrivals in Australasia and Polynesia. Many rubiaceous genera have attained very wide distributions owing to ready dispersability. However, family differentiation certainly took place when Africa and South America were closer, with subgroups apparently having differentiated subsequently. Rubiaceae are well represented in tropical Asia, and there are a few primarily temperate genera, including especially those of the tribes Rubieae (Galieae) and Thelygoneae. Most genera of Central and North America and the West Indies presumably have come from South America in Neogene time and more recently.

The Apocynaceae sens. lat. (including Asclepiadaceae) have a distribution pattern similar to that of Rubiaceae. Despite the presence of a few small endemic genera in Australasia, the family does not appear to be old there; most of the genera have been derived since Miocene from related tropical Asian taxa. The subfamilies and some of the tribes of Apocynoideae and Plumerioideae probably existed when South America and Africa were closer together, and the same

might even be true for Asclepiadoideae. Although there are a few temperate genera—*Apocynum*, *Asclepias*—most genera of Central and North America and the West Indies have evidently come from South America in Neogene time or more recently.

Gentianaceae may be a Laurasian group, but are well represented in Africa and in South America, mainly by unrelated genera. Menyanthaceae also appear to be Laurasian, but have achieved a wide representation in Australasia; apparently, like many water plants, they are very readily dispersed.

Fossils of these families are not known before Paleocene time (Muller, 1970). Gentianales were therefore in existence when Africa and South America were closer, and the families Loganiaceae and Rubiaceae, together with some of their subdivisions, also seem to have been present. The order evidently has reached Australasia only secondarily.

Geraniales.—Linaceae are old, with pollen of *Ctenolophon* recorded from Maastrichtian time (~ 70 m.y. BP). This genus, sole member of the subfamily Ctenolophonoideae, occurs in West Tropical Africa and Southeast Asia. In the subfamily Ixonanthoideae, *Klainedoxa*, *Desbordesia*, and *Phyllocosmus* are in tropical Africa; *Oxonanthes* in tropical Asia to New Guinea; *Irvingia* in Africa and tropical Asia; *Allantospermum* in Madagascar and Borneo; *Ochthocosmus* in tropical America; and *Cyrillopsis* in northern Brazil. They clearly are differentiates of an old West Gondwanaland plexus. Houmrioideae are mainly tropical American, but with one species of *Sacoglottis* in West Africa, to which its ancestors probably drifted. Finally, Linoideae have a number of genera in Asia, some reaching Australasia but none are endemic there; *Hugonia*, with about 40 species, shared between tropical Africa, Madagascar, and Asia; *Aneulophus* endemic in West Tropical Africa; two genera, *Hebepetalum* and *Roucheria*, endemic to South America; and the cosmopolitan *Linum*. Differentiation of the four major groups of Linaceae, often regarded as families, must have occurred when Africa and South America were closely joined, but too late for direct migration into Australia, where they are poorly represented. This is in accordance with the fossil evidence (e.g. Germeraad *et al.*, 1968: 275–6).

Ancistrocladaceae occur in West Tropical Africa and again from India and Ceylon to Southeast Asia. Two of the genera of Erythroxylaceae are endemic to Africa, whereas *Erythroxylum* itself is well represented in tropical America and on Madagascar, occurring in all three main tropical regions. It probably dispersed directly between Africa and South America in early Paleogene time.

Zygophyllaceae also have a West Gondwanaland distribution, with some genera reaching Asia and a few Australia. The North American endemics *Sericodes*, *Viscainoa*, and *Morkillia* suggest a considerable antiquity for the family there. *Viscainoa* and *Morkillia* are related to one another, whereas *Sericodes* is related to *Larrea*. In the light of this, Porter (1974) has suggested a North American origin for *Larrea*, with subsequent dispersal to South America and the evolution of three additional species there. On the other hand, the arguments of Hunziker *et al.* (1973) for a southern origin appear convincing also, and the family must ultimately be derived from the south. According to Porter (1974), two genera related to *Larrea* are southwest African (*Neoluederitzia*, *Sisyndite*),

two South American (*Metharme*, *Plectocarpa*), and one (*Sericodes*) North American. *Viscainoa* and *Morkillia* seem to be derived from a tropical American complex that includes *Guaiacum*, *Porlieria*, and *Bulnesia*, as well as the Chilean *Pintoa*, probably following a Paleogene arrival in North America (Porter, 1974). *Fagonia* is highly disjunct and evidently easily dispersed. Other genera of Zygophyllaceae north of Panama are apparently recent arrivals from South America. The preceding families, constituting the suborder Linineae, certainly differentiated in West Gondwanaland prior to the Maastrichtian.

In the next suborder, Geraniineae, most of the family radiation seems to have occurred later, with Oxalidaceae, including the genus *Biophytum*, shared between South America, Africa, and Asia. However, Geraniaceae and Balsaminaceae are primarily Old World families, Tropaeolaceae South American. The most generalized Geraniaceae, the Vivianoideae, are South American. In the suborder Limnanthineae, the only family, Limnanthaceae, is confined to western North America and is probably autochthonous.

In the suborder Polygalineae, Malpighiaceae are confined to South America, with secondary extensions to Central and North America and the West Indies, except for the subtribes Aspidopteryginae (7 genera, 79 species) in Africa and Asia, with one widespread tropical species just reaching tropical Queensland; and Sphedamnocarpinae (6 genera, 45 species), also in Africa and Asia, with one species of *Rhyssopteris* native in northeastern Queensland. Since these two subtribes are related respectively to the New World subtribes Mascagniinae and Banisteriinae (Niedenau, 1928), the introduction of at least two separate New World lines into the Old World, probably Africa, is suggested (W. R. Anderson, personal communication). In context, the family scarcely seems old enough to have passed more or less directly between South America and Africa, so one may perhaps visualize mid-Tertiary or Early Neogene long-distance dispersal across the South Atlantic. Both of these groups consist of plants that have winged fruits. The probability of older long-distance dispersal of the ancestors of Aspidopteryginae and Sphedamnocarpinae seems enhanced by the occurrence of one species each of *Heteropterys* and *Stigmaphyllon*, both with winged fruits and belonging to two different Neotropical genera, in West Africa; presumably their ancestors were dispersed across the South Atlantic quite recently (W. R. Anderson, personal communication).

Polygalaceae are common to South America, Africa, and tropical Asia, with the basically tropical genus *Polygala* secondarily widespread in temperate regions. The other Central and North American genera evidently were derived from South America, and *Securidaca* leaves and pollen are in the Early Miocene of Oregon (Wolfe, 1962). Trigoniaceae are in tropical South America, Madagascar, and Malaysia—an ancient relationship. Vochysiaceae, except for *Erismadelphus*, a large forest tree of tropical West Africa, are confined to tropical America. Polygalineae seem to have radiated in West Gondwanaland, but have scarcely reached Australasia. An evident exception is the well developed Australian genus *Comesperma* (Polygonaceae), closely related to if not identical with the South American *Bredemeyera*, which probably reached Australia by a cool-temperate southern route. The North American representatives of Polygalineae

consist of a few temperate genera from Eurasia with some South American additions presumably dating from the Miocene or more recently.

Hamamelidales.—Most families of this ancient and archaic group are entirely Laurasian: Trochodendraceae, Tetracentraceae, Eupteleaceae, Cercidiphyllaceae, Eucommiaceae, Platanaceae. In the Hamamelidaceae itself, the subfamilies Liquidambaroideae, Disanthoideae, Rhodoleioideae, and Exbucklandioideae are exclusively Laurasian. In the subfamily Hamamelidoideae most genera are Laurasian, and especially tropical Asian, with *Distyliopsis* in New Guinea; *Trichocladus* is endemic to tropical East and South Africa, and *Dicoryphe* is restricted to Madagascar and the Comoros. The monotypic genera *Neostrearia* and *Ostrearia* (Smith, 1958) are endemic to tropical Queensland. These two genera are quite distinct from one another and closely related to the Malaysian *Embolanthera* and *Maingaya* (Smith, 1958; P. K. Endress, personal communication) and to the African *Trichocladus*. They therefore would seem to be Miocene or more recent arrivals in Australia from Asia. The relationship postulated between the Australian genera and *Dicoryphe* of Madagascar by White (1936: 61) is not borne out by a reexamination of their characteristics (P. K. Endress, personal communication).

Hamamelidales may have originated in eastern Asia—Western North America (Wolfe, 1974) by early Upper Cretaceous time, but seem to have reached West Gondwanaland before the close of the Period. Aubréville (1970) mentions wood of Hamamelidaceae from the Saharan region from the close of the Cretaceous, and L. J. Hickey (personal communication) has suggested that the record of *Araliaephyllum* from the Cretaceous of Argentina (Menéndez, 1972) may refer to a hamamelid. The existence of the distinctive endemic *Dicoryphe* in Madagascar might reflect Paleocene or earlier migration of Hamamelidaceae—Hamamelidoideae to Africa from Laurasia. Alternatively, the group might have differentiated in West Gondwanaland, a possibility that will be clarified only with additional fossil evidence.

Lamiales.—Hydrophyllaceae are principally North American, with *Hydrolea* widespread through tropical America, Africa, and Asia. *Codon* consists of two South African species. The South American Hydrophyllaceae, with the possible exception of *Hydrolea*, all appear to have been derived in Neogene time and more recently from North America. If *Codon* is truly related to other members of the family, its distribution is extremely unusual.

Boraginaceae are mainly Laurasian and have reached the southern lands repeatedly, producing a few endemic genera—*Embadium*, *Halgania*, and *Omphalolappula* in arid portions of Australia, for example. *Wellstedia*, representing a distinct subfamily, indicates some antiquity for the Boraginaceae in Africa, as do the Ehretioideae in South America. Judging from the excellent representation of ehretiid genera in the Eocene of southern England (Chandler, 1964), and the presence of several genera in Africa (*Poskea* is better referred to Scrophulariaceae), the subfamily may have spread to South America *via* Africa by Paleogene time. Lennoaceae are North American. Hoplestigmataceae consist of two species of African trees, perhaps related to Boraginaceae.

In Verbenaceae, Chloanthoideae are mainly Australian shrubs, with some representation in Madagascar and possibly East Africa, according to Airy Shaw (1966). Stilboideae are entirely South African. Phrymatoideae are Laurasian, Nyctanthoideae tropical Asian, Caryopteridoideae Asian. Symphorematoideae are mainly tropical Asian, with *Congea* also in tropical Africa and South America. Avicennioideae consist of the widespread mangrove genus *Avicennia*. Both Verbenoideae and Viticoideae are widespread in tropical Asia, Africa, and South America, with an appreciable Laurasian element also, and a few endemic genera of Verbenoideae in Australasia. The distinctive, monotypic Lithophytoideae occur in semiarid southern Mexico (D'Arcy & Keating, 1973). Callitrichaceae are widespread water plants. Lamiaceae include the Australian Prostantheroideae and seven other subfamilies which are perhaps basically Laurasian but well represented in Africa and South America. Ocimoideae may have spread relatively early—perhaps in Paleogene time—between Africa and South America, with Hyptidinae (South America) and Plectranthinae (Old World) having evolved subsequent to the wider separation of these continents (R. M. Harley, personal communication). *Tetrachondra* (the only genus of Tetrachondroideae) occurs in southernmost South America and New Zealand.

The order Lamiales, and probably ancestral Verbenaceae and Boraginaceae-Ehretioideae, seem likely to have been in existence when Africa and South America were closer. An unusual feature of the order is the strong development of endemic subfamilies of Verbenaceae and Lamiaceae in Australia. Rather than suggesting a very early arrival there, which would be inconsistent with the apparent age of the group, this pattern may imply a Paleogene arrival with subsequent extensive radiation as subarid and semihumid habitats expanded in Australia (Raven & Axelrod, 1972).

Leitneriales.—A single species of the southeastern United States. Pollen of *Leitneria* has been reported from the Oligocene of southern England (Chandler, 1964) and seeds from the Oligocene of Siberia (Dorofeyev, 1963).

Malvales.—Fossils of Sterculiaceae and Tiliaceae are well represented in the Eocene of both Europe and the United States, with Sterculiaceae extending to the Paleocene and perhaps even Maastrichtian in North America (Chandler, 1964; Krutzsch, 1967; L. J. Hickey, personal communication). The European records include pollen of the tropical Asian Tiliaceae—Brownlowieae (Krutzsch, 1967). Tiliaceae are in the Indian Eocene (Lakhanpal, 1970). Judging by the strong representation of these families also in both South America and Africa, it seems reasonable on the basis of present evidence to assume that they were in all four continents by early Paleogene time, having spread between Europe and Africa and across a narrow Atlantic Ocean between Africa and South America. The remarkable endemic sterculiaceous genera *Fremontodendron* (California, Arizona, Baja California) and *Cheirostemon* (*Cheiranthodendron*; southern Mexico, Guatemala) are probably derived from an older Laurasian element, whereas other genera doubtless entered from South America starting in Eocene time. The subfamily Byttnerioideae of Sterculiaceae is well represented in Australia. *Keraudrenia* and *Rulingia* of this group are common to Australia and Madagascar, which they probably reached by long-distance dispersal around the Indian Ocean.

Ancestral Byttnerioideae probably reached Australia *via* a temperate Antarctic route from South America.

Bombacaceae have distinctive pollen, which has not been found before the Paleocene (Muller, 1970). They are represented in Australia only by a species of the widespread tropical genus *Bombax* and one of the primarily Mascarene and African *Adansonia*. This suggests that the single species of *Adansonia* reached that continent by long-distance dispersal in the Tertiary, contrary to our earlier view (Raven & Axelrod, 1972). Like the two families just discussed, Bombacaceae are well represented in both Africa and South America, probably passing between them by Paleogene time across a narrower Atlantic Ocean. The presence of the North American endemic *Nephropetalum* (Texas, adjacent Mexico), considered in the context of the family, suggests that the pattern for Bombacaceae might be essentially similar to that proposed for Sterculiaceae and Tiliaceae, but the apparent absence of Bombacaceae in the Eocene London Clay (Chandler, 1964), in contrast to the other two families, might lend more credence to the notion of an African–South American origin for the group. In any case, Bombacaceae were in western North America by the earliest Middle Eocene (Leopold & MacGinitie, 1972) and have been reported frequently in the North American region from that time onward (*e.g.*, Graham & Jarzen, 1969; Langenheim, Hackner & Bartlett, 1967).

A southern origin is very likely for Elaeocarpaceae, best represented in South America, southeast Asia, Madagascar, and by several endemic genera in Australia, but the family is absent on the mainland of Africa. Wood of Elaeocarpaceae is reported from the Paleocene of Patagonia and from the Tertiary of India (Petriella, 1972; Lakhanpal, 1970), and fruits are reported from the Eocene of southern England (Chandler, 1964). Since the family is represented only by the widespread and common Asian genera *Elaeocarpus* (2 species) and *Sloanea* (1 species) in Madagascar, it probably reached Madagascar by long-distance dispersal around the Indian Ocean. *Sloanea* occurs in Australia only in the northeastern tropics, and probably spread from Asia to America by long-distance trans-Pacific dispersal. *Aristotelia*, on the other hand, may have spread between Australasia and temperate South America *via* an Antarctic route, or, in view of its fleshy fruits, been carried by birds.

Malvaceae are so well represented all over the world that it is difficult to analyze their distribution. They are reported from doubtful Upper Cretaceous macrofossils (Muller, 1970), but their pollen first appears in the fossil record in the Lower Eocene (Muller, 1970), and in New Zealand by the Middle Eocene (Couper, 1960). Connections between the floras of Africa and South America are indicated by the tribe Gossypieae (*e.g.* Fryxell, 1969), but *Gossypium* and some other genera of the tribe are so easily dispersed they even occur on oceanic islands, including Hawaii. The distinctive Australasian *Plagianthus* probably came *via* a temperate Antarctic route, and in general the family does not appear old enough for more or less direct dispersal between Africa and South America.

Considering present distributions and the available fossil record, it appears most likely that the primary radiation of Malvales took place in Africa + South America in Maastrichtian time or earlier, although the alternate possibility of

a primary radiation in the north cannot yet be excluded. First Sterculiaceae, then Tiliaceae and Bombacaceae, and finally Malvaceae reached Eurasia and then North America, with direct dispersal from South to North America increasing in importance throughout the Tertiary. Elaeocarpaceae have remained almost entirely a southern group. Sphaerosepalaceae, a family of two genera and some 14 species which are endemic to Madagascar, is of such uncertain affinities (*cf.* Airy Shaw, 1966), that it should not be taken into account in arguments about the phytogeography of the order (see also Theales).

Myricales.—The single family Myricaceae appears to be Laurasian, but *Myrica* also occurs in Africa and South America (where it may be relatively recent). *Canacomyrica* consists of a single New Caledonian species; it may have no direct relationship to Myricaceae (R. F. Thorne, personal communication), but is at least a very distinct subfamily (Leroy, 1949). Macrofossils of Myricaceae are reported from the Upper Cretaceous (Muller, 1970).

Myrtales.—Myrtaceae are perhaps the oldest family in the order (Muller, 1970), possibly extending back to Cenomanian time (Penny, 1969). Unfortunately, the identification of early Normapolles-type pollen with particular families is problematical (Wolfe, 1974). The original differentiation between the subfamilies Myrtoideae and Leptospermoideae evidently took place from an ancestral stock that occupied West Gondwanaland (Myrtoideae) and Australasia (Leptospermoideae). Myrtoideae are better represented in South America than in Africa at present, and abundant in tropical Asia, where they have been joined in the Miocene and more recently by some Australasian Leptospermoideae. If the Miocene record of *Eucalyptus* in Patagonia (Frenguelli, 1953) is reconfirmed, then Leptospermoideae would be seen to have reached South America *via* Antarctica. Various South American Myrtoideae have reached Central and North America and the West Indies, where most living genera of the family seem to be newcomers. The family is known from the Eocene of Europe (*e.g.* Szafer, 1964; Krutzsch, 1967) and Colorado (MacGinitie, 1969). Pollen of *Metrosideros* is known from the Maastrichtian of New Zealand (Couper, 1960), and macrofossils are reported from Argentina (Menéndez, 1972), also in the Upper Cretaceous.

Melastomataceae evidently evolved too recently to reach Australasia more or less directly, and in that region they are evident newcomers and poorly represented. They are abundant and diverse in South America, well represented in Africa and tropical Asia, and have a few temperate genera in Laurasia (Meijer, 1972). They are evidently easily dispersed, but the original stock seems to have been in existence in Paleogene time, when Africa and South America were relatively close. Probable pollen has been reported from the Paleocene of Colombia Hammen & García de Mutís, 1966).

Lythraceae are best represented in South America, where a number of endemic genera occur, some of which (*Cuphea* is a notable example) have radiated extensively in Central America, the West Indies, and southern North America after what may have been a late Paleogene arrival in North America. There are several endemic genera in Africa, but no close relationships with those of South America, implying their long isolation. The family is well represented in Laurasia, with genera such as *Decodon*, *Lythrum*, *Lagerstroemia*, and probably *Ginorea*

having evolved in temperate or subtropical areas there. Lythraceae are known from the Eocene onward in both Eurasia and in India (Graham & Graham, 1971; Eyde, 1972a). The pattern of distribution in Lythraceae is strikingly like that in Melastomataceae, suggesting the ancestral forms were probably present in West Gondwanaland and Eurasia early, but not early enough to have reached Australia until Neogene time. Some genera are widespread aquatics.

Oliniaceae and Penaeaceae are African but not necessarily properly placed in this order (see Rao & Dahlgren, 1969); Crypteroniaceae, Punicaceae, and probably Trapaceae are Laurasian. Onagraceae seem to be chiefly Laurasian, but two of the least specialized genera, *Fuchsia* and *Ludwigia*, center in South America (–Africa?). *Fuchsia* had reached New Zealand by the Middle Miocene (Couper, 1960; Jenkins, 1971; Raven, 1973a), probably by long-distance trans-Pacific dispersal (Raven, 1973a). Early connections between North and South America are suggested by this family.

For Combretaceae (Exell & Stace, 1966, 1972), the subfamily Strephonometoideae (1 genus, 7 species) is tropical West African. In the second subfamily, Combretoideae, there are two tribes, of which the Laguncularieae consist of two widespread littoral genera, *Laguncularia* and *Lumnitzera*, and the endemic Australasian *Macropteranthus*. The second tribe, Combreteae, consists of three subtribes: (1) Pteleopsidinae (1 genus, 10 species, tropical Africa); (2) Combretinae, including three endemic African, one South American, one Asian, one African and Asian (*Quisqualis*), and one pantropical (*Combretum*) genus; and (3) Terminaliinae, including three American; one African; one Asian; one African and Asian; and two pantropical (*Terminalia*, *Conocarpus*) genera. Of the Terminaliinae, *Bucida*, with nine species, is largely centered in the tropical North American area. Combretaceae appear to provide evidence of early links between Africa and South America, both in Combretinae (even two sections of *Combretum* are common; Exell & Stace, 1972) and Terminaliinae. They are clearly newcomers to Australasia, and *Bucida* may or may not have originated in tropical North America.

Summarizing for Myrtales, the order itself and the family Myrtaceae specifically seems to be old enough to have dispersed more or less directly to Australia by a subtropical route before the full opening of the Indian Ocean. Melastomataceae, Lythraceae, and Combretaceae seem to have existed when South America and Africa were much closer. Onagraceae are mainly Laurasian, but early in South America. Myrtales apparently had become common to West Gondwanaland and Laurasia by the close of the Cretaceous, with the differentiation of families occurring in both areas. The geographical relationships accord with a pre-Eocene period of differentiation, as suggested by Muller (1970).

Nepenthes.—*Nepenthes*, the sole genus of this order, is found in tropical East Asia (and northern Australia), New Caledonia, Ceylon, the Seychelles, and Madagascar. It occurs in open habitats (see Rauh, 1973), and its small seeds are easily dispersed, so that its scattered range around the Indian Ocean may not reflect any great antiquity, any more than does its spread to northern Queensland, despite the arguments of DeJardin *et al.* (1973: 383). It is doubtless originally tropical Laurasian in origin.

Nymphaeales.—This group of widespread water plants might have originated either in West Gondwanaland or Laurasia. Leaves attributed to Nymphaeaceae are reported from the Upper Cretaceous of Argentina (Menéndez, 1972), and from the Paleocene of the Rocky Mountains and Great Plains (Brown, 1962). Remains attributed to the group are also in the Albian of the U.S.S.R. and Maryland (Samylina, 1968).

Oleales.—The three genera of Salvadoraceae all occur in Africa and tropical Asia. In the Oleaceae (Johnson, 1957), the subfamily Oleoideae has a Laurasian distribution but is very well represented in Africa, with *Notelaea* and *Nestegis* Australasian. In the second subfamily, Jasminoideae, *Menodora* (Steyermark, 1932) is in South America and South Africa, as well as North America, with one species common to South America and Africa. One species of the African and Asian *Schrebera* is known from Peru (P. S. Green, personal communication). *Jasminum* is entirely introduced in the New World (Green, personal communication). Oleaceae have considerable antiquity both in Africa and in Laurasia, where several temperate genera have evolved. They were probably not present in Africa when direct dispersal to South America was possible. This analysis implies that *Notelaea*, *Nestegis* (*Gymnelaea*), and other Australasian Oleaceae probably are to be regarded as immigrants in the Oligocene or more recently (P. S. Green, personal communication). The presence of *Nestegis* in Hawaii attests to its powers of dispersal.

Pittosporales.—The six families of the suborder Brunineae are all African, the three of suborder Pittosporineae Australasian, although *Pittosporum* ranges to Africa, Madeira, and into the Pacific as far as the Hawaiian Islands. If these groups are really homogeneous and related, the order might have considerable antiquity and may have spread more or less directly between Australia and Africa. The six families of Brunineae are placed in four different unrelated orders by Takhtajan (1969). Cronquist (1968), by placing most of Thorne's (1968) Pittosporales in Rosales, implies that there might not be a direct relationship between Thorne's subgroups. The third suborder, Daphniphyllineae, consists of a single genus of tropical Asia which may or may not belong with this group of families. The North American Stegnospermaceae, placed in this order by Hutchinson (1959), have betacyanins and belong in the Chenopodiales (Mabry, Taylor & Turner, 1963). Clearly, the Pittosporales need intensive study.

Plumbaginales.—Plumbaginaceae, first known from the fossil record in the Upper Miocene, are evidently easily dispersed, judging from their nearly cosmopolitan distribution.

Primulales.—Myrsinaceae and Primulaceae seem to have been West Gondwanaland-Laurasian counterpart families, with each having extended its range into the area of the other subsequent to their initial radiation. Myrsinaceae probably have considerable antiquity in the Asian tropics and are known from the Eocene of southern England (Chandler, 1964). *Tapeinosperma* is Australasian. The Central and North American Myrsinaceae and the South American Primulaceae presumably date from Neogene time or more recently. Theophrastaceae may have differentiated from primulalean stock in tropical North America and then spread to South America as opportunities for migration between the

continents became greater. *Clavija* is, however, a predominantly South American genus of this close-knit family, but the most advanced in the family morphologically (W. G. D'Arcy, personal communication), indicating that it may be derived from ancestors that spread to South America in or shortly before Neogene time.

Proteales.—Of the three subfamilies of Proteaceae (Johnson & Briggs, 1963 and personal communication), the most generalized, Persoonioideae, is confined to Australasia; Proteoideae to Australasia and Africa; and Grevillioideae to Australasia (reaching Fiji), Africa, and South America. It seems logical to assume that the early diversification of the family took place in warm, moist, equable forest climates in the Australasian region (Johnson & Briggs, 1963 and personal communication; Venkato Rao, 1971) from ancestors that arrived there in the mid-Cretaceous from West Gondwanaland. *Proteacidites* is a pollen type widely distributed in the Southern Hemisphere in early Upper Cretaceous time (Muller, 1970). A derivation of Proteaceae and the possibly related Laurasian Elaeagnaceae (Cronquist, 1968) from Myrtales (Cronquist, 1968) is clearly contradicted by the anatomical evidence (Eyde, 1975) and is not supported by what is known of the relative ages of the groups either. The first unequivocal records of Proteaceae pollen in the fossil record are from the Santonian (~ 82 m.y. BP) of Australasia, including New Zealand (Couper, 1960; Muller, 1970). Proteaceae and Myrtales may be derived from common rosoid ancestors no later than Early Cenomanian time (~ 110 m.y. BP; J. A. Doyle, personal communication). The pollen of Proteaceae is first known in South America from the Middle Maastrichtian (~ 68 m.y. BP) of Patagonia (S. Archangelsky, personal communication). There are no unequivocal records of Proteaceae from the Northern Hemisphere (J. A. Wolfe, personal communication; D. L. Dilcher, personal communication; Tschudy, 1971).

Some members of the subfamilies Proteoideae and Grevillioideae seem to have migrated more or less directly from Australasia to West Gondwanaland following their presumed origin in Australasia, but only Grevillioideae exist in South America at present. South American members of this subfamily belong to six distinct alliances (Johnson & Briggs, 1963, and personal communication)—(1) *Orites*, (2) *Lomatia*, (3) *Oreocallis* and *Embothrium*, (4) *Euplassa*–*Gevuina*, (5) *Roupala*, and (6) *Panopsis*. *Orites*, *Lomatia*, *Gevuina*, and *Oreocallis* are shared between Australasia and South America. The first three groups may have originated in Australasia and migrated to South America *via* Antarctica, even though *Oreocallis*, in the South American portion of its range, is confined to the northern Andes. If this reasoning is correct, then *Oreocallis*-like ancestors probably gave rise to *Embothrium* in South America. Pollen similar to that of *Lomatia* and pollen similar to that of some species of *Embothrium* is known from the Lower Paleocene of Patagonia (S. Archangelsky, personal communication).

The last three groups listed above include all the South American representatives of the tribe Macadamieae. Two species of this primarily Australasian group occur in Africa. One belongs to a monotypic genus, *Brabeium*, which occurs in relatively moist, sheltered habitats in South Africa. The second occurs in Madagascar and has been referred to the otherwise Australasian and tropical Southeast

Asian genus *Macadamia* (Capuron, 1963), but it actually represents an undescribed genus related to certain Australian genera and to the Asian *Heliciopsis*. *Macadamia*, *Brabeium*, and *Panopsis* constitute a closely related group within the Macadamieae (Johnson & Briggs, 1963, and personal communication). The South American *Panopsis* has an entirely tropical distribution and seems a most unlikely candidate to have spread between Australia and South America *via* Antarctica. In the light of the present distribution pattern, relationships, and the inferred antiquity of the group, it seems possible that the ancestors of *Panopsis* migrated directly between South America and Africa, where *Brabeium*, a member of the same lineage, survives. *Roupala*, on the other hand, which extends to southern Mexico at present, is directly related to an Australasian genus (Johnson & Briggs, personal communication), and it is difficult to ascertain the probable route of the plants of this alliance between Australasia and South America. Even though *Gevuina* is common to Australasia and South America, *Euplassa* is closely related, in some ways more primitive, and confined to South America. If the line that gave rise to *Euplassa* came to South America *via* Africa, as would be inferred from its ecology and relationships, it is now extinct in Africa, and the same might be true of the ancestors of *Roupala*. The tribe also includes *Heliciopsis*, the only exclusively Asian genus of Proteaceae, the ancestors of which presumably came from Australia in the Miocene. Our current understanding of the relationships within Proteaceae suggests that the ancestors of the Mascarene species of "*Macadamia*" came from Australia, but the timing of their arrival is uncertain.

In summary, the initial diversification of Proteaceae seems to have taken place in Australia, and then various groups seem to have migrated out by different routes and at different times: Macadamieae (Grevilleoideae) and Proteoideae to Africa in the Upper Cretaceous; at least one line of Brabeieae to South America and Africa in the Upper Cretaceous or Paleocene (tropical groups) and three to five lines of other Grevilleoideae *via* Antarctica (temperate groups), at least one by Maastrichtian time; *Macadamia*, *Helicia*, and the ancestors of *Heliciopsis* across Wallace's line in the Miocene or subsequently; and *Roupala* into the North American region at about the same time. *Gevuina* may be a genus that originated in South America and then migrated to Australia *via* Antarctica subsequently.

Rafflesiales.—Hydnoraceae exhibit an African–South American disjunction, one of the two genera being found in each region. Rafflesiaceae are basically a Laurasian family which reached South America and Australasia probably in the Miocene or more recently (*Pilostyles*), and, probably by long-distance dispersal, South Africa (*Cytinus*). Both families consist of fleshy parasites.

Rhamnales.—Elaeagnaceae are Laurasian, with one species just reaching the northern tip of Australia. Rhamnaceae are so well represented both in tropical and temperate regions that it is difficult to trace the history of the family. A number of genera of Rhamnaceae, some endemic, occur in Australasia.

Rosales.—In the large saxifragalean alliance, the elements of which are often accorded family status, the subfamilies Pentthoroideae, Saxifragoideae, Ribesioideae, Lepuropetaloidae, Parnassioideae, Pterostemonoideae, and Hydrangeoideae (Stebbins, 1972) are essentially Laurasian, with many genera having reached South America in Neogene time or more recently. Vahlzioideae

and Montinioideae are African groups, Francooideae, Columellioideae, and Phyllonomoideae are South American. Escallonioideae are South American and Australasian, presumably having migrated between the two areas *via* Antarctica, and *Tetracarpaea* (Tetracarpaeoideae; monotypic; Tasmania) may be a derivative of this line in Australasia. The Laurasian *Itea* and the African *Choristylis* constitute the Iteoideae. Brexioideae are shared between East Africa and the islands in the western Indian Ocean (*Brexia*, *Roussea*) and New Zealand (*Ixerba*), presumably reflecting ancient dispersal between these areas before the major opening of the Indian Ocean. Eremosynioideae, consisting of a single Australian annual species, are very distinctive in the Saxifragaceae s. lat.

Chrysobalanaceae have a distribution that suggests direct migration between South America and Africa, as well as to Asia and eventually Australia. Rosaceae are mainly Laurasian, but the existence of the ancient and archaic *Quillaja* and *Kageneckia* in South America; the Neuradoideae in Africa; and three isolated woody genera of the tribe Sanguisorbeae—*Margyricarpus*, *Tetraglochin*, and *Polylepis*—in South America with other comparable genera in Africa including *Bencomia* of the Canary Islands, suggest connections between South America and Africa. *Acaena* presumably evolved from primitive Sanguisorbeae in South America and later spread widely around the Antarctic region (Moore, 1972; Raven, 1973b). *Hesperomeles* is a genus of Maloideae which evidently originated in tropical North America and migrated into northwestern South America in Neogene time. Relationships of the South American *Quillaja* and *Kageneckia* to one another and to various northern genera are of interest; if they are related to the North American *Vauquelinia*, *Lyonothamnus*, and *Lindleya* (Banwar, 1966), a very early example of sweepstakes dispersal of their ancestors to South America would be inferred. No related genera are found in Africa.

Connaraceae have a West Gondwanaland pattern, and seem to have migrated between Africa and South America in Paleogene time, and to Asia; they are poorly represented in Australasia. In the Fabaceae, both Mimosoideae and Caesalpinioideae have distributions like Connaraceae, whereas Faboideae have radiated more extensively in Laurasia. Although the family is easily dispersed and offers perplexing patterns of distribution, it may well have originated or at least undergone its primary radiation and differentiation into three subfamilies in West Gondwanaland (R. M. Polhill, personal communication). The subsequent history of the family has been marked by frequent interchange between Northern and Southern Hemispheres, and the gradual accumulation of a strong representation of all three subfamilies in Australasia, probably commencing in Paleogene times. There are no reliable Cretaceous records of Caesalpinioideae (Germeraad *et al.*, 1968; J. A. Wolfe, personal communication). *Hymenaea* (Caesalpinioideae), which is spread easily in sea drift and is common to tropical Asia, Africa, and South America, had become established in Chiapas, Mexico, by the close of the Oligocene and was producing amber (Langenheim, 1967). It also occurs on many islands in the West Indies. The tribe Cynometreae, to which *Hymenaea* belongs, provides evidence of close links between Africa and South America (Langenheim, 1973).

Crassulaceae have had their principal radiation in Africa, but are also well developed in Laurasia, with some nearly cosmopolitan. Scarios calyces that have been compared with those of *Dudleya* are reported from the Eocene of California (MacGinitie, 1969); their identity needs to be confirmed. Droseraceae are so widespread that it is especially difficult to trace their history; their pollen does not appear in the fossil record until the Miocene (Leopold, 1969), but *Aldrovandra*, a widespread aquatic of Eurasia and tropical Australasia, was represented by two species in the Eocene of southern England (Chandler, 1964). Podostemonaceae have a West Gondwanaland distribution, with extensions to tropical Asia. Styliaceae are Australasian, with secondary extensions to temperate South America and tropical Asia. Their distribution, and that of the Australian Cephalotaceae, does not accord well with Thorne's (1968) placement of these families in his Rosales. Coriariaceae, despite the fact that they are best represented in New Zealand, may be Laurasian, possibly exhibiting the sort of pattern discussed by Raven (1973a) for *Fuchsia*. *Coriariopsis* is recorded from the Maastrichtian of Alberta (Srivastava, 1970), but the single existing New World species of *Coriaria* might nevertheless have spread north from South America following long-distance transport from New Zealand *via* Tahiti. Diapensiaceae and Crossosomataceae are definitely Laurasian, Greyiaceae southern African.

One of the suborders of Rosales, Cunoniaceae, deserves special attention. Cunoniaceae not only have a West Gondwanaland distribution (but without extensions into Asia), they are apparently old enough to have spread more or less directly to Australasia by a subtropical route. Even the genus *Cunonia*, admittedly loosely held together, is found in South Africa and New Caledonia. On the other hand, the very distinctive pollen grains of Cunoniaceae appear in the record in New Zealand only in Lower Miocene time (Couper, 1953). Paleocene wood of Cunoniaceae is known from Patagonia (Petriella, 1972). Pollen very similar to that of the South American genus *Lamanonia* is reported by Hickey (1974) from the Early Tertiary Golden Valley formation of North Dakota, indicating an early arrival in the north, presumably by sweepstakes dispersal. Among the rest of the group, Brunelliaceae are South American, Davidsoniaceae northeast Australian, Eucryphiaceae Australasian-South American, Corynocarpaceae restricted to the southwest Pacific and Medusagynaceae, probably better referred to Theales, confined to the Seychelles. Staphyleaceae evidently represent an ancient Laurasian derivative of this suborder, which otherwise has remained mainly southern.

The pattern of distribution in Rosales suggests that the group may have been in existence before the major opening of the Indian Ocean. The ancestors of the Saxifragaceae s. lat., including Brexioidae, and Cunoniaceae seem to have differentiated very early. Of later origin, but in existence in Paleogene time, when Africa and South America were much closer, were the Chrysobalanaceae, Connaraceae, Mimosoideae, Caesalpinioidae, Podostemonaceae, and perhaps Rosaceae and Faboideae. A number of the other groups originated early enough to migrate more or less directly between South America and Australasia *via* a cool temperate East Gondwanaland (Antarctic) route.

Rutales.—Since Rutaceae are well represented in South America, Africa, Eurasia, and Australasia, they may have originated early enough for more or less direct migration to Australia. Paleocene wood is known from Patagonia (Petriella, 1972), and the family is well represented in the Eocene of southern England (Chandler, 1964). Simaroubaceae probably also migrated more or less directly between Africa, South America, and Asia, where the temperate *Ailanthus* evolved. Whether the ditypic endemic *Cadellia* and the related monotypic endemic *Guilfoylia* in Australia are ancient elements seems doubtful in view of their ecology. The presence of the endemic *Holacantha* and *Recchia* in Mexico and the adjacent United States suggests the pattern found in Zygophyllaceae. On the other hand, Simaroubaceae are represented by three genera in the Hawaiian Islands and the family is presumably readily dispersed. Surianaceae consist of a single species widespread on tropical shores. Wood of *Suriana* has been reported from the Eocene of Wyoming (Kruse, 1954). Cneoraceae include one species of *Cneorum* in the Mediterranean region, one in Cuba, as well as the closely related monotypic *Neochamaelea* in the Canary Islands.

Meliaceae are tropical Asian, African, and South American, and clearly newcomers in Australasia. *Guarea*, common to tropical America and Africa, was present by the Maastrichtian in North America (Graham, 1962), presumably having arrived *via* Africa and Europe. There are many North American Tertiary records of *Cedrela* from the Paleocene onward. Meliaceae are also well represented in the Paleogene of southern England (Chandler, 1964). Burseraceae share this pattern of distribution, but the presence of perhaps half of the species of *Bursera* in Mexico, Central America, and the West Indies suggests that they may have some antiquity both in North and in South America. Amber in the Eocene London Clay is thought to have been produced by burseroids (Langenheim, 1969), and the family is reported from the Eocene of North America (MacGinitie, 1969). Fruiting structures similar to those of *Bursera* are well represented in the Paleogene of southern England (Chandler, 1964).

Anacardiaceae have a pattern of distribution similar to Simaroubaceae, with *Euroschinus* and *Rhodospaera* endemic in Australia, *Cyrtocarpa*, *Comocladia* and several other genera endemic to Central America, southern North America, and West Indies. The mainly South American *Tapirira* is known from the Oligo-Miocene Chiapas amber of southern Mexico (Langenheim, 1964). Anacardiaceae are reported from the Cretaceous of Argentina (Menéndez, 1972) and are represented in the Paleogene of southern England (Chandler, 1964) and Oregon (Scott in Chandler, 1964: 58). Sapindaceae are again similar, but well represented in Australasia, and reliably known from North America in the Eocene. Pollen of Sapindaceae appears in New Zealand in Paleocene time (Couper, 1960). The family is well represented in the Paleogene of southern England (Chandler, 1964). Juglandaceae and Rhoipteleaceae, constituting the suborder Juglandineae, are Laurasian, and Juglandaceae reached South America only in late Neogene time (Brown, 1946). Cenomanian records of Juglandaceae (Muller, 1970) are very doubtful, but the evolutionary line leading to this family had diverged by the Early Campanian (~ 80 m.y. BP; Wolfe, 1974). *Rhoiptelea* is known from Maastrichtian pollen (Wolfe, 1974).

Of the remaining families related to Sapindaceae, Sabiaceae are predominantly Asian and tropical American. *Meliosma* (Beusekom, 1971) is in tropical Asia and tropical America, but was widespread throughout Laurasia in Paleogene time. Of the three species of subg. *Kingsboroughia*, two are Asian, and the third, *M. alba* (Schlechtend.) Walp., disjunct in southeast Asia and southern Mexico. Paleogene and Neogene fossils representing this subgenus occur in North America and Europe, as well as in Japan (Beusekom, 1971). In subg. *Meliosma*, sect. *Meliosma* is entirely southeast Asian, but sect. *Lorenzanea* is South American. The genus *Ophiocaryon* is also endemic in South America. North American Tertiary fossil leaves which are compared by Beusekom (1971) with sect. *Lorenzanea* may all belong to sect. *Meliosma*, as do the most of North American fossils. Beusekom (1971) has considered sect. *Lorenzanea* (as well as the genus *Ophiocaryon*) as autochthonous American taxa, but that does not solve the problem of how they reached South America. Presumably this distribution could have been achieved most easily *via* Africa, where the family is not now represented, but where it may well be found in the fossil record. Thus *Meliosma* subg. *Meliosma* may have reached Mexico by two routes, one *via* Africa, the other by way of Beringia or, more probably, the North Atlantic. If a critical evaluation of the North American fossils definitely establishes the existence of sect. *Lorenzanea* in North America, then very early and unlikely long-distance dispersal to South America might be postulated; how *Ophiocaryon* or its ancestors arrived in South America would still pose a difficult problem.

Melanthaceae are African, the monotypic Akaniaceae, Australian. Aceraceae are Laurasian. Hippocastanaceae are also Laurasian, *Billia* evidently having migrated into Colombia in Pliocene time or more recently. Breitschneideraceae are Chinese.

Much of the primary differentiation of Rurales seems to have taken place in Africa-South America, with long-standing connections to Eurasia. It appears possible that at least Rutaceae and Sapindaceae, and probably Simaroubaceae and Anacardiaceae, had appeared early enough (Turonian?) for more or less direct migration to Australia. Several families of Rurales include relict genera in the North American region, suggesting early differentiation in semiarid sites in Laurasia.

Salicales.—The single family, with three genera, is clearly Laurasian.

Santalales.—Celastraceae are widely distributed in temperate and tropical regions, including Australasia, and evidently relatively easily dispersed. They are reported from Cretaceous macrofossils (Muller, 1970), but not known from fossil pollen until the Upper Miocene. They show no obvious patterns of distribution linked with continental movements. The related Stackhousiaceae are essentially Australasian. Icacinaceae are well represented in Africa, South America, and tropical Asia, and evidently dispersed between Africa and South America when they were much closer. There are at least four endemic genera in Australasia, and pollen is reported from the Upper Cretaceous of New York State (Scott & Barghoorn, 1957), with fruits known from the Paleocene of Egypt (Chandler, 1954), and from the Eocene of Europe (Reid & Chandler, 1933; Chandler, 1964; Krutzsch, 1967) and of Oregon (Scott, 1954). *Onoana*, a

putatively icacinaceous plant from the Early Cretaceous, has been discussed on p. 560. Cardiopteridaceae are tropical Asian, Medusandraceae tropical West African, Myzodendraceae temperate South American and parasitic.

Olacaceae, including some genera, are common to South America and Africa, extending into tropical Asia, as in Icacinaceae. The living North American Olacaceae may have come from South America or be derived from Laurasian ancestors. The family was in Europe (Chandler, 1964; Krutzsch, 1967) and in Oregon (Scott *in* Chandler, 1964: 58) in the Eocene. Curiously, pollen of the *Anacolosidites* type is known from the Paleocene of Australia (Harris, 1965). The pollen is very distinctive and resembles that of *Anacolosia*, *Cathedra*, and *Ptychopetalum*, a group that appears to have had a West Gondwanaland-Asian history. It is known from the Maastrichtian of North America (Srivastava, 1970), the Paleocene of Victoria, Nigeria, and northern Asia, and from Borneo, but it is not in the Caribbean region until the Paleocene-Eocene transition (Germeraad *et al.*, 1968). This pollen type has since become less abundant in all areas. This suggests that despite their occurrence in Australia, which is confined to the principally recent Asian arrivals *Olex* and *Ximenia*, Olacaceae migrated to Australia more or less directly before the close of the Cretaceous, then became extinct.

Opiliaceae are common to tropical South America and Africa, and also reach tropical Asia. Santalaceae are widely distributed in tropical and temperate regions, including Australasia. Loranthaceae (Barlow & Wiens, 1971) appear to be basically a south temperate group which evolved in South America and Australasia, and then spread north through Asia and then southward into Africa in the Tertiary. In contrast, Viscaceae (Wiens & Barlow, 1971) appear to be a Laurasian group which has spread southward into Africa, South America, and Australia. This pattern would imply the evolution of *Korthalsella* in tropical Asia and of *Phoradendron* and *Dendrophthora* in tropical North America. Eremolepidaceae (Wiens & Barlow, 1971) are South American, with secondary spreading into Central and North America presumably in the Miocene and more recently. This family may be derived from Santalaceae.

Balanophoraceae may not be directly related to the other families in the order (R. F. Thorne, personal communication). The subfamily Lophophytoideae is South American, the subfamilies Balanophoroideae and Helosidoideae South American, African, and tropical Asian, and with extensions into Central America and tropical North America probably no older than the Miocene. *Balanophora* (Hansen, 1972) is tropical Asian, with one species extending from West Africa to Tahiti and another found in Rarotonga, so dispersal may not be difficult in this group. *Langsdorffia* is common to tropical America and New Guinea (Geesink, 1972). The subfamilies Mystropetaloidae and Sacrophytoideae are African, whereas the two genera of Dactylanthoideae are found one each in New Caledonia and New Zealand. Balanophoraceae, which may be a heterogeneous group bound together by only a superficial similarity (Airy Shaw, 1966: 114), seem nevertheless to have had a West Gondwanaland-tropical Asian history. The related Cynomoriaceae are Eurasian.

Santalales evidently radiated in West Gondwanaland, migrating in the Upper Cretaceous to tropical Asia, and very likely reaching Australasia early, judging

from the representation of Santalaceae, Icacinaceae, and Balanophoraceae, as well as the endemic Stackhousiaceae, there.

Sarraceniales.—The three genera of Sarraceniaceae occur, respectively, in western North America, eastern North America, and the Guianas. The direction and timing of their migration between North and South America is unknown.

Solanales.—Solanaceae, evidently easily dispersed and often with berries, occur widely in tropical and temperate regions. The geography of the family provides no indications of great antiquity, although the ancestors of *Duboisia*, *Anthotroche*, and *Anthocercis* presumably reached Australasia *via* Antarctica from South America in Paleogene time. Indeed, the weak representation of Solanaceae in Africa—if not due to Neogene extinction—would seem to indicate major differentiation in South America in isolation, although there are several distinctive Laurasian elements. Solanaceae are known as fossils from the Eocene (Muller, 1970). Convolvulaceae are widespread but exhibit no apparently ancient patterns. Polemoniaceae and Fouquieriaceae are groups that differentiated in semiarid North America bordering the tropics, with Polemoniaceae reaching South America probably in the Miocene or more recently and Eurasia perhaps in the Pleistocene. The ancestors of *Cobaea* may have differentiated in tropical North America, whereas *Cantua* and *Huthia* must have differentiated from *Bonplandia*-like ancestors following relatively early long-distance dispersal to South America (Grant, 1959). The pollen of this family first appears in the fossil record in the Miocene (Leopold, 1969). Differentiation of families of Solanales may have occurred after the wide separation of Africa and South America.

Tamaricales.—Frankeniaceae are readily dispersed in alkaline situations and along shores. Perhaps they are from a South American, or South American–African homeland; *Beatsonia* is endemic on St. Helena and *Hypericopsis* in Iran. About 50 species of the widespread *Frankenia* are recognized in Australia. Tamaricaceae are clearly Eurasian.

Theales.—Dilleniaceae (Stebbins, 1972) are best developed in diversity and number of species in Australasia, with good representation also in South America and in tropical Asia. The Hibbertieae are Australian, but one species of *Hibbertia* is in Madagascar and *Schumacheria*, perhaps the most archaic and unspecialized genus in the family (Dickison, 1967*a, b*), is in Ceylon. The ancestors of *Schumacheria* might have been carried northward with the Indian Plate, as suggested for *Hortonia* (Axelrod, 1971). If the very primitive monotypic *Didesmandra* of Borneo is referable to Hibbertieae, as suggested by G. L. Stebbins (personal communication), the occurrence of *Hibbertia* in the Eocene London Clay might not seem so anomalous. On the other hand, *H. coriacea* Baill., the only species of the genus in Madagascar, occurs in open coastal woods (Rauh, 1973) and is closely related to West Australian species. It is reasonable to assume it reached Madagascar by long-distance dispersal. Dillenieae and Acrotremeae are basically tropical Asian, with *Dillenia* also reported from the Eocene London Clay (Chandler, 1964). Tetraceae are South American but with a few species of *Tetracera* in the Old World tropics, including Africa, and reported from the Eocene London Clay (Chandler, 1964) and several Eocene to Early Oligocene

floras on the Pacific Coast (see MacGinitie, 1937: 148). Thus the Dilleniaceae appear to be a very old family, with tribal differentiation having followed the opening of the Indian Ocean and the separation of South America from Africa.

Paoniaceae, Actinidiaceae, Stachyuraceae, and Pentaphylacaceae are clearly northern groups. Only one section of *Saurauia* (Actinidiaceae; Hunter, 1966) is found in the New World, and it is inferred that the South American species (about 40) were derived from North American ancestors starting in mid-Tertiary time. *Saurauia* seems clearly to be a Paleogene arrival in North America from Eurasian sources. Theaceae also seem basically to be a northern group, but the Bonnetioideae are disjunct between South America, especially the Guyana Highland, and Malaysia, where the genus *Ploiariium* occurs. *Ternstroemia* has two African species, in addition to many in America and Asia (Hepper, 1968). *Melchiora* and the peculiar and isolated monotypic *Ficalhoa* are endemic to Africa.

Aquifoliaceae are widely distributed, but most diverse in Laurasia. The genus *Ilex*, known from Maastrichtian pollen (Muller, 1970), may have migrated more or less directly between South America and Africa, but evidently is easily dispersed, judging from its presence on Hawaii and New Caledonia. The New Caledonian *Phelline*, on the other hand, may belong with Araliaceae (Airy Shaw, 1966), or elsewhere. Marcgraviaceae, Caryocaraceae, Quinaceae are South American, with evidently recent incursions into Central America. *Clethra*, the only genus of Clethraceae, consists of two sections (Sleumer, 1967). Of these, sect. *Clethra* is Laurasian, with 23 species in eastern Asia and two in the eastern United States. Sect. *Cuellaria* has two subsections, one consisting of a single species of Madeira and Tenerife (Bramwell, 1972), the second of 37 species in tropical America, about half each north and south of Panama. Leaves of sect. *Cuellaria* occur in the Lower Eocene Chalk Bluffs flora of California (MacGinitie, 1941, as *Laurophyllum litseaefolia* MacGinitie) and in the Miocene of southern California (Axelrod, 1939). This pattern suggests either the former presence of sect. *Cuellaria* on the African or Eurasian mainland, or very unlikely long-distance dispersal from the Americas to the Macronesian Islands; in any event, its occurrence in South America seems clearly to be secondary and derived from tropical North America in or perhaps even before Neogene time.

Cyrillaceae are basically North American, known from the fossil record as far back as the Upper Cretaceous (Thomas, 1960), but reported from the Paleogene of southern England also (Chandler, 1964). Two of the genera include single species which occur in South America and probably spread there in the Miocene or more recently.

Scytopetalaceae and Dioncophyllaceae are West Tropical African, Sarcolae-naceae and Sphaerosepalaceae (see also discussion under Malvales) confined to Madagascar, Medusagynaceae to the Seychellas, and Strasburgeriaceae to New Caledonia. Dipterocarpaceae are mainly tropical Asian, with one species (of *Vateria*) in the Seychelles and the very distinctive genera *Monotes* and *Marquesia*, constituting one of the two subfamilies, in tropical Africa. Hypericaceae s. lat. (Clusiaceae) are well represented both in the remnants of West Gondwanaland and in tropical Asia, being known from fruits in the Eocene of India (Lakhanpal, 1970). *Symphonia* and *Vismia* common to Africa, Madagascar, and South Amer-

ica, which *Symphonia* at least reached by long-distance dispersal (Germeraad *et al.*, 1968: 277–8). *Rheedia* is common to tropical America and Madagascar, and *Hypericum* has become widespread in temperate regions. *Montrouzieria* is endemic to New Caledonia, which, especially in view of its relationship to *Symphonia*, its ancestors probably reached by long-distance dispersal. Lecythidaceae have had a similar history but remained wholly tropical in distribution. The differentiation of major groups within the family seems to have followed the separation of Africa and South America. Thus Lecythidaceae–Lecythidoideae are entirely American; Barringtonioideae, widespread in Old World tropics; Napoleonoideae, West Tropical Africa; Foetidoideae, Mascarene region; and Asteranthoideae (monotypic), Brazil. Elatinaceae are widespread waterplants.

Summarizing for Theales, both West Gondwanaland and tropical Laurasia appear to have been important sites of evolution, with the Dilleniaceae apparently reaching Australasia *via* a warm temperate to subtropical pathway in the mid-Cretaceous, as did the ancestors of Strasburgeriaceae and perhaps *Oncotheca*, if it belongs in this order (Takhtajan, 1969). Hypericaceae may also have reached Australasia very early. A number of thealean lines originated in or have become confined to the Northern Hemisphere, but the Theaceae proper have differentiated both in West Gondwanaland and in Laurasia, judging from the presence of the endemic Bonnetioideae in South America, and the occurrence of a few species of Theaceae in Africa at the present time (Hepper, 1968). The South American Marcgraviaceae, Quinaceae, and Caryocaraceae and the African Scyttopetalaceae, Dioncophyllaceae, and Sarcolaenaceae may be autochthonous, having differentiated after the separation of Africa and South America. Hypericaceae, on the other hand, have a pattern of distribution which suggests more or less direct dispersal between the two continents.

Urticales.—Moraceae and Urticaceae differentiated in South America, Africa, and Laurasia, but are poorly represented in Australasia. Ulmaceae were derived from the same stock in Laurasia, and *Ulmus*-like pollen occurs in the Rocky Mountain Maastrichtian (Wolfe, 1974). Barbeyaceae, consisting of a single species of Arabia and northeastern Africa, are a group of uncertain affinities (R. F. Thorne, personal communication). There are likewise temperate genera of Moraceae and Urticaceae that have differentiated in Laurasia. Although early records of fossil Moraceae are badly in need of review, the geographical distribution of the family suggests that it was in existence early enough to have been dispersed more or less directly between Africa and South America (Axelrod, 1972c).

MONOCOTYLEDONEAE

Alismales.—The widespread water plants of the Butomaceae, Alismataceae, and Hydrocharitaceae are well represented in Laurasia and in Africa. Easily dispersed, they present no evidence either for early migration to Australasia or for direct connections between Africa and South America, where their representation is poorer than in Africa.

Arales.—Araceae appear to have a West Gondwanaland–Laurasian distribution that has been interrupted by much extinction in Africa. Pollen is reported

from the Paleocene of Colombia that may be *Spathiphyllum* (Hammen & García de Mutís, 1966). The tribes Pythonieae, Philodendreae, Colocasieae, Dieffenbachieae, and Richardieae link Africa and South America, several extending to Asia also. *Philodendron* sect. *Meconostigma*, now confined to South America, is reported from the Middle Eocene of Tennessee (Daghlian & Dilcher, 1971; Dilcher, 1973b). There are a number of temperate Laurasian genera, and the family may be relatively old in Australasia, at least as judged from the presence of the distinctive endemic genus *Gymnostachys*. Lemnaceae and Typhaceae are widespread waterplants. Sparganiaceae are Laurasian and probably recent arrivals in Australasia.

Arecales.—The palms probably originated in West Gondwanaland, with subsequent decimation in Africa and migration to Eurasia and ultimately Australasia, where several arecoid alliances have proliferated (Moore, 1973a, 1973b). Authentic palm fossils go back to the basal Campanian (~ 80 m.y. BP; Read & Hickey, 1972; Scott *et al.*, 1972; Moore, 1973), following which coryphoid palms, fairly uniform, soon became frequent. Palms are known from the South American Senonian (Menéndez, 1969; Muller, 1970), and from the central Patagonian Danian (~ 64 m.y. BP), a warm temperate period (Romero, 1968). The genus *Nypa* was in existence and widespread in the Maastrichtian (Germeraad *et al.*, 1968; Tralau, 1964, 1968; Muller, 1970). Most Central American and Mexican palms seem to be recent arrivals from South America, whereas most coryphoid palms in North America probably are Laurasian elements (H. E. Moore, Jr., personal communication). *Pseudophoenix*, most distinctive of the North American palms, may have arrived in Paleogene time from South America, but the direction and time of arrival of many other palms in the North American region is problematical. There is no sign of great antiquity for the palms of Australasia or of the Pacific (H. E. Moore, Jr., personal communication), although they appear in both New Zealand (Couper, 1960) and Australia (McWhae *et al.*, 1958: 133) in the Eocene.

Commelinales.—Bromeliaceae are South American, with probably Miocene and more recent extensions into Central and North America and the West Indies. The single species of *Pitcairnia* on the seaciffs of West Africa undoubtedly reached them by long-distance dispersal. Rapateaceae are another primarily South American group, but the monotypic semiaquatic genus *Maschalocephalus* is confined to West Africa, which its ancestors probably reached in Neogene or later times by long-distance dispersal. It is closely similar to other members of the tribe Monotremeae (Carlquist, 1966). Xyridaceae are easily dispersed and widely distributed, especially in the tropics; the few Australian species of *Xyris* may have arrived recently. Pontederiaceae are easily dispersed waterplants centering in South America and Africa, but with *Monochoria* ranging more widely and *Pontederia* in North America. It is difficult to say whether the family existed or not when more or less direct communication between Africa and South America was possible; there are four common genera and one endemic to each continent.

Philydraceae are Australasian, one genus ranging into Southeast Asia. Much of the diversity of Juncaceae is in South America, but the widespread temperate *Juncus* and *Luzula* probably differentiated in Laurasia. The Antarctic genera

probably originated in southern South America and then spread by long-distance dispersal. Cyperaceae are now so widespread and numerous that their distribution is difficult to analyze. They are well represented in South America, Africa, tropical Asia, and Australasia, and have numerous temperate genera also. The most primitive subfamily, Mapanioideae, exhibits a West Gondwanaland-Laurasian range, and it is especially well represented in the Guyana Highlands (Maguire, 1971).

Commelinaceae are well represented in the West Gondwanaland continents and in Asia, but are apparently readily dispersed (Brenan, 1966; Tomlinson, 1966; Jones & Jopling, 1972). The same suggestion might be made for such genera as *Murdannia*, *Floscopa*, and *Aneilema*. Although the remarkable *Cartonema* is restricted to northern Australia, the family does not in general appear to have any great antiquity there. All genera north of Panama, except perhaps *Thyr-santhemum* and a few others, may have been derived from South America in Neogene time and subsequently. *Mayaca*, the only genus of Mayacaceae, has about 10 primarily South American species and one in Angola, a distribution that can be explained most easily by long-distance dispersal. Eriocaulaceae are waterplants well represented in Africa and South America, with *Eriocaulon* more widespread. North American representatives, including the endemic *Lach-nocaulon*, have probably been derived from South America. Flagellariaceae occur in tropical Asia, with *Flagellaria* ranging to Africa and Australia, and *Joinvillea* to the Pacific. Restionaceae are reported from Eocene fossil pollen in Europe (e.g. Chandler, 1964; Krutzsch, 1967), but the environment does not seem to have been suitable, and these records should be carefully reviewed. They probably passed between Africa and Australasia by long-distance dispersal in Paleogene time, reaching southern South America subsequently, also by long-distance dispersal (Cutler, 1972; Raven & Axelrod, 1972), but in any case are probably no older than the Maastrichtian at most (Doyle, 1973). Centrolepidaceae are basically Australasian and Subantarctic in distribution.

Among the Poaceae, the ancient and archaic Bambuseae, although pan-tropical and well represented on Madagascar, are very poorly represented in continental Africa and virtually absent from Australia. Many of the more specialized groups of the family probably originated in Laurasia following migration from Africa into Eurasia, whereas many archaic and unspecialized grasses are confined to, or radiated from, Africa. The relatively unspecialized olyrioid grasses are mainly South American, whereas other lines of grasses seem to have radiated principally from Asia. Very few especially unspecialized or unusual grasses occur in Australasia (*Micraira* is one exception), where the family is probably not an ancient element. The bamboos found north of Panama, except for the Laurasian *Arundinaria* and *Yushania* (McClure, 1973), probably arrived in the Neogene time or more recently from South America. Some of the South American bamboos may be found to be related to those of Africa and Madagascar, and their ancestors may have migrated between these continents when they were closer together. It is difficult on phytogeographic grounds to accept a direct relationship between the primarily South American *Guadua* and the Asian *Bambusa*, as proposed by McClure (1973, see comment by R. E. Holttum, pp. v-viii),

although Lardizabalaceae have a similar distribution. Grass pollen has not been detected in New Zealand prior to the Pliocene (Couper, 1960), possibly because of a wider forest cover on the east side of the South Island prior to the uplift of the main range. Pollen of the family is first reported from the Maastrichtian of West Africa (Muller, 1970; Doyle, 1973), but grasses do not become frequent in the fossil record until the Lower Eocene, probably correlated with the rise of grazing mammals and the origin of non-bambusoid tribes of grasses (J. Muller, personal communication).

In summary, most of the families of this order seem to have differentiated in the Guyana Shield area of South America, as suggested by R. F. Thorne (personal communication). It is difficult to be sure which if any of the families of the order existed early enough for direct dispersal to Africa, although the bambusoid grasses are likely candidates. Some alliances reached Australasia a very long time ago, judging from the existence of Philydraceae, Centrolepidaceae, and especially Restionaceae, but the facility with which modern members of the order seem to be spread by long-distance dispersal makes it difficult to know when and how their ancestors may have reached Australia, especially if the Paleogene pollen records of Restionaceae in Europe are correct.

Cyclanthales.—Cyclanthaceae are South American, and have spread northward probably in the Miocene and more recently. They may have originated from a common West Gondwanaland stock with Arecaceae, which is consistent with their reported occurrence in the Paleocene of India (Sahni & Surange, 1953; Lakhanpal, 1970).

Liliales.—Following the analysis of Huber (1969), Liliaceae of Thorne (1968) would be divided into eight orders. Among the smaller ones, Dioscoreales (Dioscoreaceae, Stenomeridaceae, and Trichopodaceae) are Laurasian and African, but there are a number of South American species of *Dioscorea* (including *Epipetrum*). *Dioscorea* might have spread more or less directly between Africa and South America (Ayensu, 1972) or reached South America early by sweepstakes dispersal from the north. Roxburghiales (Roxburghiaceae, Trilliaceae) are Laurasian. Taccales (Taccaceae) are evidently Laurasian, and especially east Asian, but a few species of *Tacca* occur in Africa and Madagascar, and a few others occur in South America. Since the genus is also in Hawaii, it seems unwise to attribute this pattern of distribution to great age. In Haemodorales (Haemodoraceae), the Conostylideae are Western Australian, Haemodoreae South American and African, with *Haemadorum* (mainly Western) Australian and one species in Malaysia. The North American *Lophiola* seems not to belong with the conostylid Haemodoraceae, but rather with the colchicoid Liliiflorae, near *Alettris* (Huber, 1969). Velloziales (Velloziaceae) are confined to South America and Africa (Ayensu, 1973), and they evidently existed when these continents were close together. If the close relationship between Velloziaceae and Bromeliaceae postulated by Huber (1969) is confirmed, it might be possible to think of the group as a whole as having originated in West Gondwanaland, with subsequent differentiation of Bromeliaceae after the wider separation of South America and Africa. On the other hand, Taccaceae and Haemodoraceae, said by Huber to be related, appear to have differentiated respectively in the north and in the south.

In the Orchidales, the saprophytic Burmanniaceae are evidently easily dispersed and nearly cosmopolitan. We can say nothing useful about their distribution, except that they are predominantly tropical. Nearly the same statement can be made for the vast and readily dispersed family Orchidaceae, which unfortunately lack a useful fossil record (Schmid & Schmid, 1973). The two least specialized subfamilies, Apostasioideae and Cyripedioideae, however, are Laurasian, and mainly east Asian, this possibly suggesting their area of origin. Orchidaceae are much better represented in South America and tropical Asia than in Africa, and more diverse and abundant on Madagascar than in continental Africa, a frequent pattern.

One of the major hypotheses of Huber (1969) is the separation of the asparagoid Liliiflorae (as Asparagales). Eight family groups are recognized, and these will now be reviewed in turn:

(a) Asparagaceae alliance: Ripogonaceae (*Ripogonum*), Australasia, Smilacaceae (*Smilax*, *Pseudosmilax*, *Heterosmilax*), evidently easily dispersed, with *Smilax* on Hawaii, but perhaps Laurasian. Philesiaceae (*Lapageria*, *Philesia*), temperate South American. Luzuriagaceae, mainly Australasian, but with *Luzuriaga* in Chile and New Zealand, and the monotypic *Behnia* endemic to southeastern Africa. Ruscaceae, Laurasian and North African. Convallariaceae, Laurasian with the two species of *Drymophila* endemic to eastern Australia and Tasmania. Dracaenaceae (*Dracaena*, *Sansevieria*), Old World tropics, especially Africa, the Canaries, one species of *Dracaena* just reaching northern Australia. Nolinaceae, drier portions of North America. Asparagaceae, widespread in warmer and drier portions of Old World, and one species native to Australia. Herreriaceae, one genus in Madagascar, another one or perhaps two in South America. This alliance appears to be widespread and of some antiquity. Only Herreriaceae, however, seem to have been involved in more or less direct dispersal between Africa and South America, which makes it seem likely that the ancestors of Luzuriagaceae may have reached Australia *via* Antarctica from South America, and those of *Ripogonum* and *Drymophila*, both with fleshy fruits, from the warmer parts of the Old World by long-distance dispersal. This is almost certainly the case for the few Australian species of the widespread genera *Smilax*, *Dracaena*, and *Asparagus*. *Behnia*, which likewise has a berry like all Luzuriagaceae, is probably derived from ancestors that reached Africa by long-distance dispersal also.

(b) Asteliaceae alliance: Asteliaceae consist of the primarily Australasian *Astelia* and *Milligania* (the former evidently easily dispersed and ranging out into the Pacific to Hawaii), and with one species in southern South America, together with *Cordyline*, which is widespread in the Asian and American tropics, as well as northern Australia and New Zealand, where it first appears in the fossil record in the Lower Miocene (Couper, 1953). *Cohnia*, with three species, occurs in the Mascarene Islands and on New Caledonia; it has berries and probably reached the Mascarene Islands by long-distance dispersal from the east. Dianellaceae are likewise Australasian, with the berry-fruited *Dianella* ranging to tropical Asia, Madagascar, and Hawaii, and the capsule-fruited *Excremis* South American, possibly having reached that continent by way of an Antarctic route. Hypoxidaceae seem to center in Africa, and to have spread to Asia and eventually the

New World from there. *Hypoxis*, of which most species occur in Africa, and *Curculigo* are widespread. If the relationship between Velloziaceae and Hypoxidaceae discussed by Ayensu (1973) is genuine, then the case for an African origin would be strengthened. The monotypic and distinctive South African *Lanaria* is likewise allied by Huber (1969) with this group. The families of this alliance seem to suggest long-standing connections between Africa and Australasia, but it is difficult to say why if they are so old they are so poorly represented in South America.

(c) Tecophilaeaceae alliance: *Walleria* and *Eriospermum*, each assigned by Huber (1969) to its own family, are African. In the Tecophilaeaceae, *Cyanella* is South African, three other genera Chilean, and the monotypic Californian *Odontostomum* probably also correctly referred here according to Huber. Old connections between Africa and South America seem to be indicated, but how and when the ancestors of *Odontostomum* reached California is uncertain.

(d) Xanthorrhoeaceae alliance: Australasian, diverse and probably ancient.

(e) Asphodelaceae alliance: Many genera, widespread but much better represented in the Southern Hemisphere; both tropical and temperate (Antarctic?) connections between South America and the Old World seem to be represented in this group, and the Johnsonieae are evidently of considerable antiquity in Australia, as are the distinctive genera *Sowerbaea* and *Bartlingia*.

(f) Phormiaceae alliance: Australasian, probably ancient. Pollen of *Phormium* is known from the Middle Eocene onward in New Zealand (Couper, 1960).

(g) Agavaceae alliance: Subhumid to arid portions of the North American region, except for the East Asian *Hosta*. Presumably an ancient Laurasian group.

(h) Amaryllidaceae-Hemerocallidaceae alliance: Hemerocallidaceae consist only of the Eurasian *Hemerocallis*, with about 20 species. Alliaceae are mainly South American, with some genera in North America, especially western North America, and *Allium* widespread in the Northern Hemisphere. Agapanthaceae are South African. Hyacinthaceae consist of three tribes, the western North American Chlorogaleae, the African Bowieae, and the African-Mediterranean Scilleae, with *Camassia* endemic to North America and the monotypic *Fortunatia*, closely related to the Old World *Scilla*, in Chile, which its ancestors must have reached by long-distance dispersal. Amaryllidaceae in the strict sense are African, South American, and Laurasian, with several groups having genera in both Africa and South America. Eustephieae are entirely South American, and Hippeastreae are South American and Laurasian. The impression is of a group that has considerable antiquity both in South America and in Africa, and doubtless dispersed between these continents when they were much closer than at present. This alliance has evidently also been represented in Laurasia for a very long time. The disjunction in range between the Alliaceae-Brodiaeeae in North and South America is unusual.

For Asparagales (Huber, 1969) as a whole, West Gondwanaland seems clearly to have been the primary site of evolution, with Laurasia involved probably before the close of the Cretaceous. The ancestors of elements among the families related to Asteliaceae, Xanthorrhoeaceae, Asphodelaceae, and Phormiaceae seem to have reached Australasia early, whereas elements in the groups related to

Asparagaceae, Asteliaceae, Tecophilaeaceae, Asphodelaceae, and Amaryllidaceae—Hemerocallidaceae suggest old connections between Africa and South America. The kind of disjunctions in range between North and South America that occurs in Alliaceae—Brodiaeeae and Tecophilaeaceae is unusual among angiosperms as a whole and suggests ready dispersibility for these plants.

For the colchicoid Liliiflorae, grouped by Huber (1969) as Liliales s. str., Melanthiaceae are Laurasian except for *Nietneria* of northern South America. Calochortaceae, consisting of a single genus, are western North American and Mexican. Liliaceae s. str. (Tulipeae) are Eurasian and secondarily North American. Colchicaceae are Eurasian and African, with several small genera in Australia and Tasmania (which they probably reached independently by long-distance dispersal) and one (*Uvularia*) in North America.

Iridaceae probably were in existence when South America and Africa were closer, and they have had their principal radiation on these continents. Some genera are Eurasian—*Hemerodactylus*, *Belemcanda*, *Gladiolus*, *Crocus*, for example—and *Iris*, a Eurasian genus, has reached North America at least twice. Primitive Iridoideae, as well as some Sisyrinchioideae, are shared between Africa and South America, also implying the origin of these subfamilies by Paleogene time, and probably a more recent origin for the third subfamily, the basically African Ixioideae (P. Goldblatt, personal communication). No genera or even tribes are common to Africa and South America, in spite of misconceptions to this effect based on faulty taxonomic treatments (P. Goldblatt, 1971). *Sisyrinchium*, *Tigridia*, and the ancestors of the endemic *Rigidella* were evidently recent arrivals in North America. The Australasian Sisyrinchieae have probably been derived from South America *via* Antarctica, as might the ancestors of *Patersonia* (Aristeae) and those of the New Caledonian *Campynemanthe* (Huber, 1969) and the Tasmanian *Isophysis* (*Hewardia*). How the single endemic species of the otherwise African *Dietes* reached Lord Howe Island is problematical. One of the most remarkable Iridaceae is the saprophytic *Geosiris* of Madagascar, which is relict and implies antiquity.

The Liliales s. str. (colchicoid Liliiflorae) do not appear, on the basis of present distributions, to be as old as the Asparagales (sensu Huber, 1969). Only Iridaceae seem to be old enough to have migrated more or less directly between South America and Africa (Paleocene?), with the other groups all more recent.

Despite the fact that many of the members of this large array of families and perhaps orders are easily dispersed, it does appear likely that ancestral forms related to this order existed when more or less direct migration into Australia for warm temperate plants was possible. Pollen of the group appears in New Zealand about 70 m.y. BP (Couper, 1960). Primitive Liliaceae, Amaryllidaceae, Haemodoraceae—Haemodoreae, Iridaceae, and Velloziaceae seem to have existed when South America and Africa were more closely linked, whereas most of other groups may not yet have originated. The major differentiation of the complex as a whole may perhaps have been in West Gondwanaland, but Roxburghiales, Taccales, the colchicoid Liliiflorae (Liliales s. str.), and Orchidales seem to have had their primary radiation in Laurasia, as do many smaller groups. Early migration to Australia is suggested for the ancestors of some groups, notably the

Xanthorrhoeaceae alliance, the Phormiaceae alliance, the Johnsonieae, and the Asteliaceae alliance, all asparagoid Liliiflorae (Asparagales); and for the ancestors of Haemodoraceae-Conostyloideae. Other groups appear to have arrived in Australia more recently, by long-distance dispersal, or (as in Iridaceae) *via* Antarctica from South America. The kinds of disjunction in range between North and South America in Brodiaeae and Tecophilaeaceae are unusual for angiosperms as a whole and, together with other evidence, suggest that many members of the Liliiflorae are very easily dispersed.

Najadales.—A single genus of widespread waterplants.

Pandanales.—Pandanaaceae are now widespread in the Old World tropics, but are not necessarily old in Australasia. The order has affinity with Cyclanthaceae and Arecaceae and may have a Cretaceous age.

Triuridales.—Triuridaceae occur in South America, Africa, and Asia and are herbaceous saprophytes. The species north of Panama and in Australasia are clearly recent arrivals, and the plants of this unique and specialized family appear to be easily dispersed. The genus *Sciaphila* has nearly the entire range of the family.

Zingiberales.—Musaceae almost certainly antedate the separation of South America from Africa, with clear-cut endemic genera in both areas and no ready means of dispersal. *Musa* ranges to tropical Asia. A *Heliconia*-like stem with attached lamina occurs in the Paleocene of India (Trivedi & Berma, 1972). Most species of *Heliconia* are tropical American, but one is Melanesian (Green, 1969), possibly having crossed the Pacific by long-distance dispersal as has been hypothesized for other fleshy-fruited genera such as *Fuchsia* (Raven, 1973a) and *Coriaria*. Lowiaceae, acaulescent herbs represented by a single genus *Orchidanthera*, are endemic to Malaya and Borneo.

Zingiberaceae are mainly confined to Africa and tropical Asia, but *Renealmia* (Zingibereae) and *Costus* (Costeae) are common to Africa and South America. The other genera of Costeae are also South American, except *Tapeinocheilos* which ranges from tropical Asia to Australia. The family is recorded from the Eocene of southern England (Chandler, 1964) and India (Prakash, 1972: 80), and the Early Eocene of North America (Hickey, 1974). The family probably was common to Laurasia and West Gondwanaland very early. Cannaceae are South American, but spread to Laurasia by Early Tertiary time, judging from the occurrence of leaves probably referable to this family in the Eocene of North America (Berry, 1916, 1924) and the Soviet Union (Gorbunov, 1962), and in the latest Oligocene of Montana (Becker, 1969).

In the Marantaceae one of the two tribes, Phrynneae, is found in Africa and tropical Asia, except for *Calathea* of South America; the other, Maranteae, is South American, except for *Thalia*, one species of which occurs in tropical Africa and in tropical America, the other ten being confined to tropical America. Marantaceae seem to have existed prior to the separation of South America and Africa, and these seem clearly to have had 3-locular ovaries and therefore to have been referable to the tribe Phrynneae. The family is recorded from the Eocene of southern England (Chandler, 1964). *Calathea* and the Maranteae seem to

have evolved in South America after its separation from Africa, and *Thalia geniculata* L. has probably been carried back to Africa by long-distance dispersal.

Zosteriales.—What has been said for Alismales can be repeated for most of this order, Potamogetonaceae, Posidonaceae, Zannichelliaceae, and Zosteraceae. The presence of two endemic genera related to *Triglochin* in Australia and one in southern South America is interesting, and the ancestors of Juncaginaceae (Scheuchzeriaceae)—Juncaginoideae may have had a relatively long history in Australia. Aponogetonaceae are Asian and African, but known from the Upper Cretaceous of Patagonia (Selling, 1947), indicating their antiquity and past history.

ANGIOSPERM BIOGEOGRAPHY

We shall now review the patterns of distribution just discussed in the light of plate tectonic events reviewed earlier to see what can be learned about the age and pattern of dispersal of various angiosperm groups. A major obstacle in such considerations is posed by the possibility that some of the recognized orders are "unnatural;" *i.e.* did not have a common ancestor which gave rise to the families presently included in the order. Nonetheless, students of angiosperm phylogeny are converging on standard definitions of the orders, and the current evidence supports most of the groupings; exceptions will be discussed at the appropriate points. We shall now consider some of the characteristic patterns of angiosperm distribution that have been perceived in our review.

DISPERSAL BETWEEN AFRICA AND SOUTH AMERICA

General.—Explanations for the taxa to Africa and South America have fallen in one of three groups: 1) long-distance dispersal; 2) land bridges; 3) sea-floor spreading. For example, some plant geographers assert that all of the links between the far-flung tropical lands of the western Pacific and America, or between America and Africa, can be explained by long-distance dispersal. While in no way denying the importance of such dispersal (Axelrod, 1952*a*; Iltis, 1967; Sauer, 1969; Raven, 1963, 1973*a*, 1973*b*; Bowden *et al.*, 1971; Johnson & Bowden, 1973), we feel that many of the presumed examples are more readily explained in terms of sea-floor spreading (Axelrod, 1970, 1972*a*).

In his excellent and detailed analysis of the relationships between Africa and South America, Thorne (1973*b*) did not take into sufficient account the differing ages and rates of evolution of the taxa involved; the gradual opening of the Atlantic, with opportunities for migration between Africa and South America being greater at any time in the past than they are now; and the high degree of impoverishment of the African flora by climatic change during the Neogene and Quaternary.

Much of the confusion involved in discussions concerning the dispersal of plants and animals between Africa and South America stems from the natural desire to find one absolute answer to the question of long-distance dispersal *vs.* direct migration. Thus Thorne (1973*b*) and Iltis (1967) have attempted to ascribe all close similarities in the floras of South America and Africa to long-distance dispersal. The question is, however, a relative one.

As we have already seen, these continents parted company about 100 m.y. BP. Sea-floor spreading data show that in Early Paleocene time (~ 64 m.y. BP), they were about 800 km apart. This is a third more than the distance between Yucatán and Jamaica, which has in about 15 m.y. acquired a flora of some 2,888 species of angiosperms, representing 996 genera (Adams, 1972), a number of species of *Eleutherodactylus*, four species of *Hyla*, many lizards, some snakes, an extinct primate, an octodont rodent, and various other animals (Darlington, 1957). If such exchange had taken place between Africa and South America into the Paleocene, today we would be unable to distinguish its results from those of direct overland migration.

Islands have probably been present in the position of Hawaii for at least 70 m.y. (Dalrymple *et al.*, 1973), yet they were farther from the present position of North America in the past because the latter has been moving west from the mid-Atlantic ridge. They are now about 3,900 km from North America, the closest source area. At least 272 flowering plant immigrants have become established in the Hawaiian Islands (Fosberg, 1948), including such families as Apocynaceae, Aquifoliaceae, Araliaceae, Arecaceae, Asteraceae, Campanulaceae, Celastraceae, Cucurbitaceae, Cyperaceae, Euphorbiaceae, Fabaceae, Gesneriaceae, Goodeniaceae, Hydrangeaceae, Lamiaceae, Liliaceae (*Smilax*, *Cordyline*), Loganiaceae, Myrsinaceae, Myrtaceae, Orchidaceae, Piperaceae, Poaceae, Rhamnaceae, Rubiaceae, Rutaceae, Sapindaceae, Sapotaceae, Theaceae, Thymelaeaceae, Urticaceae, and Violaceae. Many of these are, of course, from source areas other than North America, and farther removed from Hawaii. This does not mean that long-distance migration to Hawaii was entirely over open tracts of water of such magnitude. The numerous archipelagos of the Southwest Pacific no doubt provided important stepping stones in the past, the high islands having been since eroded to wave level, and thence transported subsea by sea-floor spreading (Axelrod, 1972a: fig. 25).

Aside from the fact that it is easier to become established on new volcanic islands in the ocean than on a continent with an existing flora, the plants of Hawaii illustrate very clearly the potentialities of long-distance migration. The distance of the Hawaiian Islands from the nearest mainland is about 60 per cent greater than the present distance between Africa and South America. Yet these figures should not be taken to prove or disprove the mode of dispersal of a single group, or of all groups, between distant lands. In our analysis of the floras of Africa and South America, we have tried to identify those groups for which a sufficient antiquity was plausible or demonstrated, and for which the representation on the two continents indicated more or less direct migration in Paleocene or earlier times. At these times, there would have been numerous islands along the Mid-Atlantic Ridge that would have served as stepping stones between Africa and South America.

Steenis (1962), on the basis of much more limited geological information than we have at our disposal today, once called on land bridges to explain the fundamental relations between the tropical flora of America and that of Southeast Asia-Malaysia. More of the genera and families of tropical South America are common to Southeast Asia-Malaysia than to Africa (Thorne, 1973a). Since the

Paleocene separation of Africa from Eurasia, migration, *via* the North and Central Atlantic and the Bering Straits, has been much more direct between tropical America and Eurasia than between Africa and either other continent. Although the problem of migration of tropical plants through the north is a difficult one, some migration of such plants by such a route apparently has certainly taken place, and the climates in the north were definitely warmer in the past (Wolfe, 1972; Smith *et al.*, 1973; McKenna, 1973; Thorne, 1973*a*, 1973*b*). On the other hand more or less direct migration between South America and Africa provided a simpler possibility for exchange between the Old and New World tropics into Paleogene times and must also be given serious consideration.

The earlier belief of Thorne (1973*b*), Smith (1973), and others, that separation of Africa-South America had been completed before the appearance of present seed plant floras of the world, and possibly earlier than that of the Jurassic gymnosperms, is supported neither by botanical nor by geological evidence. The gradual isolation of tropical Africa from South America by progressive sea-floor spreading during the Late Cretaceous and Tertiary preceded the origin of many new taxa (genera, tribes, families) in each area (Axelrod, 1970; 1972*a*). That the distinctness of the tropical flora on opposing shores of the Atlantic increased during the Cenozoic is demonstrated by the presence of essentially identical pollen floras in the Late Cretaceous of Brazil and Gabon (Freake, 1966), and very similar ones in Colombia and Nigeria (Hoeken-Klinkenberg, 1964), as compared with the marked differences between them today. Brenner (1974) groups northern South America and Africa in a single floristic province in the Upper Cretaceous. Even in the Early Tertiary, Krutzsch (1967) considers South America, Africa, and India to constitute a single province from the standpoint of palynology. Numerous islands afforded ready migration across the opening Atlantic into the Early Tertiary. As these commenced to subside, and as the ocean basin deepened and widened, long-distance dispersal gradually became more important.

The breakup of West Gondwanaland by sea-floor spreading led to the increasing distinctness of the floras and faunas of Africa and South America. Relations of this sort are inferred for such groups as mites, land mollusks, fresh-water fish and insects, liverworts, and other alliances that are common to South America-Africa, and to other tropical regions, as summarized recently by various authorities (*in* Fittkau *et al.*, 1968, 1969). At the same time, there was an increasing tendency for the marine faunas of the Caribbean region to become distinct from those of the Mediterranean region (see Hallam, 1973*a*; Douglas *et al.*, 1973; papers in symposium volumes edited by Mindelmiss, Rawson & Newall, 1971; Hughes, 1973; and Keast, Erk & Glass, 1973, for example). The marked differences between the American-African tropical floras are due in large measure to their evolution in isolation (Axelrod, 1970), as well as to widespread extinction in Africa (Axelrod, 1972*a*, 1972*c*).

At the generic level, a recent review of the relationships between Africa and South America has been provided by Thorne (1973*b*). At least 111 genera of Africa and Madagascar are limited to Africa-Madagascar and America, representing fewer than 2.5 per cent of the genera of both continents. However, as can be seen repeatedly in the preceding pages, any genus or other group old

enough to have spread directly between Africa and South America would also have had direct access to Eurasia. Therefore, it is not particularly meaningful to limit comparisons only to those taxa restricted to Africa and America. Interestingly, about 45 endemic genera in Africa-Madagascar have more than 100 species (Thorne, 1973*b*). Clearly, most of these originated since the separation of Africa and South America. On the other hand, some relatively old—*e.g.* *Guarea*, *Caperonia*—and some recent—*e.g.* *Aspilia*, *Coreopsis*, *Chrysocoma*—genera are represented by large numbers of species on both continents. This clearly implies that opportunities for evolutionary bursts may be recurrent for genera of woody plants—though not for the placental mammals which evolved into new genera. In some cases, as Velloziaceae (Ayensu, 1973), older taxonomies have given mistaken impressions about the representation of intrafamilial groups on the two continents (see also Johnson & Briggs, 1963; Cutler, 1972). Statistical analyses of floras are interesting, but can be judged adequately only in the context of the careful examination of individual groups.

Direct Migration.—The groups noted below presumably migrated between Africa and South America during or prior to the Paleocene, judging from what is known or can be inferred about their history and from their present patterns of distribution. After the Paleocene, the floras of Africa and South America became largely distinct, and the evidence suggests only limited migration between these continents from the Eocene onward (Germeraad *et al.*, 1968). The profound differences between the floras of Africa and South America led Engler (1905) to reject the notion of any connection in the past. Some long-distance dispersal has occurred throughout the Tertiary, however, and doubtless is still occurring. The age of genera such as *Solanum* and *Gossypium*, both represented on Hawaii, which is some 60 per cent farther from the nearest source area than Africa is from South America, cannot be dated from the original separation of these continents, as proposed by Hawkes and Smith (1965). The notion that either long-distance dispersal or direct migration is responsible for all the African-South American similarities is in error. Virtually all of the groups listed are also known or presumed to have reached Eurasia by the Early Paleocene, and many are well developed in Eurasia and/or North America at present:

Annonales, including Annonaceae, Canellaceae, Myristicaceae, Siparunaceae, Monimiaceae s. str., and Lauraceae (including *Ocotea* and *Beilschmeidia*).

Arales, Araceae (several tribes).

Arecales, Arecaceae (several subgroups).

Berberidales, Menispermaceae.

Bignoniales, Bignoniaceae, including Tecomeae, with Bignonieae s. str. and other tribes arising subsequently; Gesneriaceae, with the split between Cyrtandroidae (Old World) and Gesnerioideae occurring subsequently.

Capparales, Capparaceae.

Chenopodiales, possibly Phytolaccaceae, the other families evidently having evolved more recently after the separation of Africa and South America. Basellaceae and Portulacaceae-Calandrineae are also common to both continents, but may have evolved more recently.

- Cistales, Flacourtiaceae (including Oncobeeae, Banareae, Homalieae), Cochlospermaceae (*Cochlospermum*), Turneraceae, Caricaceae, Cucurbitaceae (including Anguriinae; Jeffrey, 1962).
- Commelinales, Poaceae (bambusoid grasses only).
- Cornales, Rhizophoraceae, Araliaceae, Apiaceae–Hydrocotyloideae.
- Ebenales, Ebenaceae (*Diospyros*), Sapotaceae (including *Manilkara* and pentasepalous groups; Aubréville, 1973), Styracaceae.
- Ericales, Ericaceae [including Andromedeae (Gaultherieae)].
- Euphorbiales, Euphorbiaceae, Dichapetalaceae (including *Tapura* and *Dichapetalum*), Thymelaeaceae, Buxaceae–Stylocereae.
- Gentianales, Loganiaceae–Desfontainioideae, Loganioideae; Antoniaceae; Strychnaceae (including *Strychnos*); Rubiaceae; Apocynaceae, including Apocynoideae and Plumerioideae; possibly Gentianaceae.
- Geraniales, Linaceae (including subfamilies Ixonanthoideae and Linoideae), Erythroxylaceae (*Erythroxylum*), Zygophyllaceae, Oxalidaceae, Malpighiaceae, Polygalaceae, Vochysiaceae.
- Liliales, Amaryllidaceae–Hemerocallidaceae, Asphodelaceae, Dianellaceae, and Herreriaceae, Tecophilaeaceae, Amaryllidaceae (several tribes), Haemodora-ceae (including Haemodoreae), Velloziaceae, Iridaceae.
- Malvales, Sterculiaceae, Tiliaceae, Bombacaceae.
- Myrtales, Myrtaceae–Myrtoideae, Melastomataceae, Lythraceae, Combretaceae (including Combretinae and Terminaliinae).
- Primulales, Myrsinaceae.
- Proteales, Proteaceae, tribe Macadamieae.
- Rafflesiales, Hydnoraceae.
- Rosales, Chrysobalanaceae; Rosaceae–Sanguisorbeae; Connaraceae; Fabaceae–Mimosoideae and Caesalpinioideae, possibly including the tribes Swartzieae and Cynometreae, as well as *Macrolobium* and *Bauhinia*, among others; Podostemonaceae; Cunoniaceae.
- Rutales, Rutaceae, Simaroubaceae, Meliaceae (including *Guarea*), Burseraceae, Anacardiaceae, Sapindaceae.
- Santalales, Balanophoraceae, Icacinaceae, Olacaceae (including *Heisteria*), Opiliaceae.
- Theales, Dilleniaceae, Theaceae (including *Ternstroemia*), Aquifoliaceae (*Ilex*), Hypericaceae (perhaps including *Rheedia* and *Vismia*), Lecythidaceae.
- Urticales, Moraceae and Urticaceae.
- Zingiberales, Musaceae (including Strelitzioideae), Zingiberaceae (including Costeae, *Costus*, and *Renanthera*), Marantaceae (including Phrynneae).

Probably a majority of families and many modern genera of seed plants had come into existence by the Paleocene. Many of these seem to have dispersed more or less directly between Africa and South America. There is also an almost complete floristic continuity at the family and often generic level between Africa and Southeast Asia, indicating the ease of migration between these two areas into early Paleogene time (Axelrod, 1960: 257–258), and again in the Neogene

when the overland connection was restored, though by the later Miocene the links were chiefly those of drier climates.

A number of families not on the list above appear to have evolved more recently, or to be so easily dispersed that they may have spread between South America and Africa by long-distance dispersal, as of course may some of those listed above. These include: Cyperaceae, Juncaceae, Celastraceae, Convolvulaceae, Orchidaceae, Solanaceae, and Xyridaceae, for example, as well as the genera *Menodora* and *Fagonia*, among many others. In some taxa, a single species apparently has been carried from one continent to the other: Houmirioidae (Linaceae), *Thalia* (Marantaceae–Maranteae), Bromeliaceae, Rapateaceae, Cactaceae (two apparently derived species coexist with the original one in Madagascar; Guillaumet, 1972), *Maranthes* (Chrysobalanaceae; Prance, 1968). The occurrence of a single genus, *Codon*, of the predominantly North American Hydrophyllaceae, in South Africa, can most easily be explained in this manner, although alternative possibilities involving extinction in intermediate areas cannot be ruled out.

A very interesting case deserving special comment concerns *Parkia* (Fabaceae–Mimosoideae; Baker, 1973). Common to all three main tropical regions of the world and bat-pollinated in each, *Parkia* might have migrated more or less directly, although there is very little evidence that Mimosoideae could be so old. *Parkia* is pollinated by the exclusively Old World Megachiroptera in the Old World, by the cosmopolitan Microchiroptera in the New World (Baker, 1973). Evidently the Megachiroptera evolved well after the separation of Africa and South America, whereas *Parkia* probably evolved earlier.

Arid Areas.—When South America and Africa were in close contact, there must have been extensive arid areas, some of them edaphic, in the interior of the vast continent formed by their union (Axelrod, 1972*a*, *b*; Schuster, 1972). This has been demonstrated by the Cretaceous saline deposits of the Sergipe basin of Brazil and the Gabon basin of Africa by Allard and Hurst (1969) and is evident from the present geology of the areas concerned. Many of the endemic families and taxa of the two continents may have survived in, or later evolved in, such edaphic deserts, including unique xerophytic endemics in such families as Velloziaceae and Bombacaceae which link Africa and South America (Axelrod, 1970, 1972*b*). Much of the *primary* differentiation of Chenopodiales, producing such families as the American Cactaceae and Portulacaceae, and the African Didiereaceae and Aizoaceae, may well have taken place in such local edaphic settings.

Nonetheless, there is no evidence to support the contention of Engler (1914) that genera such as the following, which are scattered in arid regions around the Atlantic basin, owe the disjunctions in their ranges to the breakup of West Gondwanaland: *Menodora* (Oleaceae), *Fagonia* (Zygophyllaceae), *Thamnosma* (Rutaceae), *Pilostyles* (Rafflesiaceae), *Frankenia* (Frankeniaceae), *Lycium* (Solanaceae), and various Chenopodiaceae (*Atriplex*, *Chenopodium*, *Salsola*), and Fabaceae (*Acacia*, *Hoffmanseggia*, *Prosopis*). For the most part they are not isolates within their families, and they comprise only a very small proportion of the floras of the areas in which they occur, although *Acacia* is a clear exception.

Some occur in Australia (*Frankenia*, *Acacia*, *Lycium*, *Atriplex*, *Chenopodium*, *Suaeda*), in which the evolution of arid areas has taken place in complete isolation from all others (Raven & Axelrod, 1972). As pointed out by Raven (1973a), they must have attained both their disjunct east-west and north-south ranges by long-distance dispersal. As we have seen, those plants which may have occurred in these arid areas since the time of separation of Africa and South America have subsequently become distinct genera or even families. Long-distance dispersal between similar climatic regions in Africa and South America has probably occurred, but with decreasing probability, ever since separation (Simpson, 1952; Axelrod, 1952a; Raven, 1973a). As the continents separated, their climates would have become moister and more equable (Axelrod, 1972b), and hence the probability of long-distance dispersal between the contracting arid areas would have decreased. On the other hand, so much air-borne dust, doubtless including many seeds and small animals, is being blown westward from Africa that the sun is being dimmed over the Caribbean region and as much as 15 per cent of the solar energy reaching the surface of the tropical Atlantic may be lost (Anonymous, 1974). This condition clearly indicates the efficacy of winds for such intercontinental transport. Increasing opportunities for the evolution of rainforest and savanna taxa would have developed on these continents in Upper Cretaceous and Paleogene times, supporting Stebbins' hypothesis (1952) that taxa of rainforest environment may have been derived from those of drier areas.

In contrast to the relationships between the southern lands, migration between North America and Eurasia has been relatively unimpeded during most of the history of the flowering plants. The North Atlantic provided an overland pathway for plants of temperate forested regions until 49 m.y. BP and an interrupted one into the Miocene (*i.e. via* Iceland); the Beringian area has been equally important and the sole major land route since the Eocene. These pathways account for the sort of patterns discussed by Sharp (1966), Graham (1972), Hara (1972), Thorne (1973a), Wood (1973) and many others, but are not important for the plants of subhumid to semiarid habitats (Raven, 1971, 1973a). The sorts of differences between the pollen floras of eastern North America and Europe from the Cenomanian onward may be related to the relatively high latitude of the bridge between the two continents (Wolfe & Pakiser, 1971). As Kornaś (1972) has pointed out, the herbaceous species of the boreal coniferous forests are often circumpolar, but those of the deciduous woodland are older and hence generally are clearly separated taxonomically.

Many genera of woody plants are common to the Mediterranean region and California, playing conspicuous roles in the vegetation of both regions. These are reviewed by Raven (1971) and include *Acer*, *Arbutus*, *Cercis*, *Clematis*, *Cupressus*, *Fraxinus*, *Juniperus*, *Lonicera*, *Platanus*, *Populus*, *Prunus*, *Rhamnus*, *Rhus*, *Rosa*, *Rubus*, *Smilax*, *Staphylea*, *Stryax*, *Viburnum*, *Vitis*, and especially *Pinus* (with "closed-cone," fire-type species in each area) and *Quercus* (with a number of very important and conspicuous evergreen oaks in each region). The ties were even more numerous in Neogene times, with such genera as *Clethra*, *Ilex*, *Ocotea*, *Persea*, *Pistacia*, *Sabal*, and *Sapindus* present in each region (Axelrod, 1972a, 1973). Most of them are also found in the Eocene, and MacGinitie (1941)

has also reported *Nerium* of the Mediterranean region from the Eocene of California. Many of these genera have been associated with the Arcto-Tertiary Geoflora and its derivatives since at least Paleogene time, and they have differentiated similar species in semiarid areas on the two sides of the Atlantic. Only in Late Miocene time did the semiarid plant communities of Eurasia (Takhtajan, 1969) and North America (Axelrod, 1950, 1958) approach their modern form.

As judged from current reconstructions which place eastern America and western Europe in latitudes suited to warm, seasonally dry climate, these taxa may have bridged the Atlantic during the Late Cretaceous to Early Eocene (Axelrod, 1972c, 1973). With scattered islands along the Mid-Atlantic Ridge and its flanks, east-west movement would be possible. On this basis, it is not surprising to find that the Azores still have a Mediterranean flora (*i.e.* *Erica*, *Ilex*, *Lavatera*, *Myrsine*, *Persea*, *Myrtus*, *Myrica*, *Rhamnus*); that the family Cneroaceae is restricted to the western Mediterranean–Canary Islands and Cuba; and that various genera (*Clethra*, *Pistacia*, *Persea*, *Myrica*, *Ilex*, etc.) in the subhumid parts of Mexico have representatives in the Neogene of California and in the Mediterranean region. All of these may be regarded as the surviving descendants of the more numerous links between the subhumid climates at the edge of the tropics on opposite sides of the Atlantic during the past. The rather numerous ties between the mediterranean regions north of the tropics (Raven, 1971) provide a marked contrast with the profound differences between sclerophyllous taxa in the regions of mediterranean climate in central Chile, Australia, and South Africa. This is wholly consistent with their much longer period of separation.

The Impoverished African Flora.—The distribution of the “primitive” woody ranalian angiosperms and other groups that reveal stronger ties between the American and Australasian tropical floras than the African, seems due largely to one factor: impoverishment of the African flora, chiefly during Neogene and later times. Down to the close of the Oligocene the African tropical flora probably was very diverse. This is implied in part by the rich flora that has survived on Madagascar which was a part of Africa until mid- or Late Cretaceous time. Furthermore, the Late Cretaceous and Paleogene rainforest vegetation of North Africa, covering what is now the Sahara Desert, included such families as Annonaceae, Celastraceae, Combretaceae, Dipterocarpaceae, Ebenaceae, Fabaceae, Hamamelidaceae, Hypericaceae, Icacinaceae, Lauraceae, Meliaceae, Moraceae, Myristicaceae, Myrtaceae, Proteaceae, Rutaceae, Sterculiaceae, and Theaceae (Aubréville, 1970, 1971; Chandler, 1954). These also included *Nypa* (Chandler, 1954; Tralau, 1964), which is now extinct in Africa. Humid forest evidently clothed nearly all of Africa, except perhaps for the south, until Neogene time.

In discussing imbalance in the African flora, Richards (1973) notes that there probably is no large area of African rainforest where rainfall is distributed evenly through the year; even in its wettest parts there is a month or two of dry season, with precipitation as low as 100 mm. Since the richest part of the rainforest flora, and that which harbors most of the relicts, regularly occurs in areas with least drought, he infers spreading drought may have eliminated numerous taxa that lived there earlier. Axelrod (1972a) noted that the development and spread of dry climate over tropical Africa probably began near the close of the Oligocene,

at which time upwarp of the continent commenced, and has continued to the present as the rift valleys continue to grow (see Baker, Mohr & Williams, 1972, for new geologic evidence). The altitude of eastern Africa has increased fully 8,000 feet above that of the Miocene (in Axelrod, 1972a: 50-51) and has brought to it a cooler and drier climate. This was supplemented by building a volcanic field from Ethiopia southward down the rift valleys, further increasing the rain-shadow effect and bringing greater drought and temperature extremes.

A second major factor that affected the African flora was the development of the Benguela Current, for it brings cold water and hence a drier climate to the West African coast. Since glaciation was initiated on Antarctica in the Early Miocene (Anonymous, 1973; Hayes *et al.*, 1973), cold water commenced to bathe the West African coast at that time, bringing to it a dry season of at least slight magnitude. Furthermore, in the Pliocene (~ 5 m.y. BP) glaciation on Antarctica was extensive so that the bottom of the Ross Sea was scraped by an ice sheet that extended 200-300 miles farther out than the present one (Hayes *et al.*, 1973). Whereas the Ross Ice Shelf now forms an apron of floating ice about 600 feet thick, the Pliocene ice sheet plowed across the sea floor that is 1,000 to 2,000 feet below sea level. Clearly, this would not only have brought a much drier climate to the tropical West African coast, it may also (in a global sense) account for the very dry climate of the Middle Pliocene, as recorded in California and elsewhere (Axelrod, 1948; Mudrey *et al.*, 1973).

Finally, fluctuations of Quaternary climate also had an important effect on the African tropical rainforest flora, with the drier phases being times of extinction of taxa that required more nearly ever-wet conditions (*e.g.* Langenheim, 1972). Wild (1968: 207) and others have reconstructed tentative vegetation maps of Rhodesia and other parts of Africa showing how vegetation could have differed from that of today if rainfall increased to approximately 150 per cent of present levels. The maps show that Rhodesian forests that are now isolated would have been sufficiently widespread to have been in contact with the main forest areas of the Congo and West Africa. This could explain the affinities of species and generic composition of the Rhodesian forests that are now isolated, but have West African relationships. Quaternary pluvials of only 50 per cent higher rainfall could also probably account for the distribution of middle and lower altitude riparian forest species which may have formed a more or less continuous forest at lower altitudes through much of tropical Africa. In this sense, their present isolated distributions are merely relict of their former wide occurrences along most river systems.

At the same time that spreading drought tended to impoverish and disrupt the African flora, other factors were operating that tended to preserve the richness of the South American and Australasian tropical floras. With respect to South America, it is recalled that the cold water from Antarctica that now flows north as the strong Humboldt Current is the chief cause of the Atacama Desert climate and probably also the barren desert slopes of the entire Pacific slopes of the Andes north of Santiago, Chile. From the Paleocene to Miocene, tropical to subtropical rainforest inhabited the present desert coast of Peru and Chile (review in Berry, 1938: 48). We infer that as the Humboldt Current gained strength

during the Miocene and Pliocene, and as the subtropic high became more permanent, rainforest was replaced by savanna and then thorn scrub, and finally desert vegetation. Gerth (1941) commented on the progressively increasing severity of the South American climate as reflected by the changing floras of Upper Cretaceous, Paleogene, and Neogene times. However, the Andes commenced to rise in the later Pliocene and Quaternary. They then imposed an effective barrier between the moist climate suited to the rich tropical rainforest and savanna vegetation of Brazil and adjacent tropical lands east of the range, and that suited to the expanding aridity and to thorn scrub and desert vegetation to the west. Clearly, the tropical rainforest of South America would have become further impoverished if the Andes had not sheltered it from spreading drought on the west coast. That it has suffered some impoverishment in the east is clear from the record in northeast Brazil. A rich Pliocene rainforest is recorded in Bahia (Hollick, 1924), but today the fossil locality is in a region of thorn scrub. The aridity here results in large part from the cold water carried west from Africa by the Benguela-Brazil Current which is sufficiently cold to inhibit reef corals, and accounts in large part for the low precipitation and the presence of thorn scrub there.

There is now reliable evidence for widespread ice-age aridity in low tropical latitudes (Emiliani, 1971: 185). In South America, Bigarella and de Andre (1965) note that residual pediments occur at the foot of the Serra do Mar in east-central Brazil, in present-day very wet forested areas. Since pediments and pediplanes—which form under relatively dry to desert climates—can be traced widely over eastern Brazil, they conclude that climate was semiarid, not pluvial, as had generally been supposed, when sea level was lower. They suggest that world-wide aridity probably affected wide areas of the inner tropics during the cold phases of the Pleistocene. This evidence is nicely supplemented by the discovery that arkosic sands of late Wisconsin age occur in deep sea cores from the Guiana basin, whereas today fine muds derived from deep chemical weathering are being deposited there (Damuth & Fairbridge, 1970). This observation is consistent with the nature of a pollen flora of late Wisconsin age (12,000 years BP) recovered from the deep sea off Argentina which shows that semiarid vegetation (*Ephedra*, chenopods) was widespread, and “occurred when sea level was low, and when much of the present wide continental shelf was emerged and supported a steppe vegetation” (Groot & Groot, 1966). Measurements of kaolinite/quartz ratios in Caribbean cores likewise indicate that the Caribbean area was more arid during Pleistocene temperature minima (Bonati & Gartner, 1973), as do studies of foraminiferal assemblages in the Colombia Basin (Prell, 1973). The circulation of both the California and Peru currents into equatorial regions along the west coast of South America was intensified during glacial maxima (Thompson & Saito, 1973), this necessarily resulting in increased aridity onshore.

Furthermore, biological evidence from the lowlands of Colombia and Guyana (Wijmstra & Hammen, 1966), Brazil (Haffer, 1969, 1970; Vanzolini & Williams, 1970; Vanzolini, 1970), and the Galapagos Islands (Colinvaux, 1972) can best be interpreted in terms of widespread drought and forest restriction during the glacial ages (Vuilleumier, 1971). Evidence of various taxa indicate many areas

of disjunction, hybridization, secondary sympatry, and introgression exist in Amazonia. Since these areas of secondary contact do not correspond to observable physical or ecological barriers, they must be related to historical factors. Inasmuch as these areas occur across Amazonia, which is now a relatively uniform habitat, Vuilleumier postulates that there must have been Pleistocene climatic changes that caused the fragmentation and re-expansion of the selva. The changes in the climate were presumably synchronous with those that also affected the montane forests in the lower Andes. She therefore visualizes the repeated alternation of distribution patterns during the Quaternary, with rainforests fragmented during the dry (glacial) periods and then expanding again during the humid (inter-glacial) phases. Thus, speciation of forest taxa was initiated or completed in isolated patches of fragmented forest. Secondary contract, with hybridization or reunion of populations that did not become reproductively isolated, occurred in periods of expansion. In this manner, Pleistocene climatic changes have had a major role in increasing the diversity in the inner tropics—a region that previously had been regarded as stable, an evolutionary enigma (Vuilleumier, 1971).

The phenomenon of ice-age aridity was not confined to South America. Pleistocene dune ridges (now stabilized) pass below sea level onto the continental shelf of northwest Australia. They evidently formed at a more arid, cooler time than now, when sea level was glacio-eustatically lowered and the Sahul Shelf was dry land (Fairbridge, 1953). From his study of birds in Timor and northern Australia, Mayr (1944) concluded that a dry savanna landscape on the Sahul Shelf during the glacial stages was required to permit migration of grassland birds. In New Guinea and adjacent Australia sea level was about 180 meters lower during the glacial ages, and hence more than adequate to unite Australia and New Guinea, and to extend Australia far to the northwest. Webster and Streten (1973) indicate that at these times cooler sea-surface temperatures, cooler trade winds, and the greatly expanded land surfaces gave the region a significantly drier climate than at present. This supports Mayr's inference (1969) that alternating climates during the Quaternary can largely explain much of the recent bird speciation in the tropics.

In West Africa (*in* Damuth & Fairbridge, 1970), Tricart reports that desert dunes from the Sahara dive below sea level at the coast. At the glacial maxima, the Sahara sands spread south into the Upper Nile and the Congo rivers. Radio-carbon dating of alluvial fills in the Nile and in the Congo indicate that these great tropical rivers were partly overwhelmed by desert sands and almost dried up during certain stages of the Wisconsin maximum (see Damuth & Fairbridge, 1970, for references). Bakker (1972), collating evidence provided by the late Pleistocene and Holocene lacustrine phases in the southern Sahara and in East Africa, showed that the lake levels changed practically simultaneously in the entire area. Evidence suggests desert-like conditions in the region during a time that was contemporaneous with the last maximum glaciation. He infers that the climate of the Sudan and Guinea was dry about 20,000 years ago—during the Wisconsin. By analogy, other glacial ages in the inner tropics were also dry. Bakker and Coetzee (1972), after a review of evidence of late Quaternary climate change in tropical Africa, conclude glacial-age climate was drier and interglacial-

age climate was wetter than at present, which agrees with evidence provided earlier on the bases of studies in more local areas (*i.e.* Livingstone, 1967: 50; 1968; 1971; Coetzee, 1967: 68, 81; Hamilton, 1972; Kendall, 1969). Bakker and Coetzee (1972) emphasize that during the arid and semiarid cooler phases the pattern of plant and animal distribution was greatly different than that of the present. The Sahara extended to the south, and in East and Central Africa mountain forests must have been very restricted and isolated. During winters in the glacial periods, intrusions of cool Benguela-South Equatorial Current waters occurred off north-west Africa, contributing greatly to spreading aridity in regions now tropical (Gardner, 1973). Dry types of woodland, savanna and grassland were widespread, and the main area of tropical rainforest may have been confined to local areas similar to that indicated for the Amazonian selva (Vuilleumier, 1971). Clearly, the evidence of recurrent, ice-age aridity in the tropics nicely explains many of the evolutionary problems posed by taxa in both the New and Old World tropics, as discussed recently in the symposium on *Speciation in Tropical Environments* (Lowe-McConnell, 1969) and also by Vuilleumier (1971).

The climatic vicissitudes of the Neogene (Benguela, Humboldt Currents triggering drought) and the Quaternary with several periods of ice-age aridity seem adequate to explain the impoverishment of the African flora, as well as the tropical American and presumably the Southeast Asian (and Indian) flora as well. This may well account for the elimination of taxa that may earlier have been in Africa, or America, and now survive only in Asia, or in equable insular regions that were less affected by these changes.

The several drought periods of the Quaternary not only impoverished the South American and African rainforests, but that of the area from Southeast Asia to Australasia as well, though probably in lesser degree owing to the more oceanic nature of the area. These periods of ice-age drought bring up the problem, chiefly discussed by archaeologists, geographers and botanists, as to whether tropical grasslands are man-made. The evidence of ice-age aridity in the tropics implies that at least some of them are native—not man-made—and are relicts of past climate (but see Wijmstra & Hammen, 1966). A strong indication of this is seen in the actual distribution of grasslands in the region stretching from New Guinea westward to Asia and northward into the Philippines: these are clearly controlled by terrain and climate, as judged from a study of tens of thousands of high altitude aerial photos of the entire region.

Survival and Extinction in Africa.—We have direct fossil evidence for the extinction of some plants, such as *Nypa* (Tralau, 1964), in Africa. Unfortunately, owing mainly to the general uplift of the continent from the Miocene onward, there are few Cretaceous or Paleogene rocks in which to search for fossils. For a number of plant groups there is, however, indirect evidence of extinction of at least some lines on the African mainland. For example, on Madagascar and its neighboring islands in the western Indian Ocean, groups such as ferns, palms, orchids, bamboos, Malpighiaceae, Celastraceae, and Bignoniaceae are much better represented than on the African mainland, a pattern which seems to be associated with the effects of spreading aridity and mass extinction on the mainland. As Dejardin *et al.* (1973) have stressed, the flora of Madagascar is in fact balanced

with respect to such widespread tropical groups: it is the situation in continental Africa which is peculiar. In addition there are a number of taxa that link tropical America with Madagascar, but are absent on the mainland of Africa. These include Monimiaceae s. str., Trigoniaceae, Winteraceae, Chloranthaceae, Elaeocarpaceae, *Rheedia* (Hypericaceae), *Rhacoma* (Celastraceae), *Ravenala-Phenakospermum* (Musaceae), *Phenax* (Utricaceae), *Weinmannia* (Cunoniaceae), Herteriaceae, the ceroxylid and chamaedoreoid palms (Moore, 1973a, 1973b), and the ferns *Adiantopsis*, *Trachypteris*, and *Ophioglossum palmatum* L. (Dejardin *et al.*, 1973). How did these disjunct distributions come about, and what may we infer from them?

Long-distance dispersal certainly has occurred, and is occurring, in the lands around the Indian Ocean. Thus we would postulate that some of the genera which provide links between the Australasian region and Madagascar such as *Hibbertia*, *Cohnia*, *Keraudrenia*, *Caesia* (also in South Africa), *Adansonia*, *Polypompholyx* (also in South America), and *Ascarinopsis-Ascarina*, as well as several other genera of such families as Asteraceae, Poaceae, and Cyperaceae, passed between Madagascar and Australasia in this manner. We base this contention upon the presence of the characteristic features of groups that have been dispersed by long-distance dispersal (Raven, 1963): unbalanced representation in the two floras, close relationship, occurrence in open habitats. There are also tropical Asian groups, such as *Nepenthes*, *Dillenia*, *Evodia*, *Dapania*, *Calophyllum*, *Rulingia* (also in Australia) and a number of other groups discussed by Dejardin *et al.* (1973), which seem to have reached Madagascar the same way, and which are presumed to be easily dispersed, judging from their present ranges. Some of the genera mentioned, incidentally, are represented on the Seychelles. Finally, groups such as *Fuchsia*, *Coriaria*, *Heliconia*, Myoporaceae, and Gesneriaceae-Gesnerioideae seem to have spread across the Pacific by long-distance dispersal. Some animals, and even iguanid lizards, may have done the same. It can clearly be seen that the disjunctions between Madagascar and tropical America could have been built up stepwise in the same way; the judgment of whether they were or not depends upon the analysis of particular taxa.

The groups linking Madagascar with tropical America differ in their overall distributions and patterns of relationship. Thus Trigoniaceae consist of two American genera, *Trigonia* (30 species) and *Lightia* (2 species), together with one monotypic genus each in Malaysia (*Trigoniastrum*) and in Madagascar (*Humbertiendendron*). Chloranthaceae appear to have reached Madagascar from the east, since the relationships of *Ascarinopsis* are with the Asian-Australasian-Polynesian *Ascarina*, and *Hedyosmum*, the only genus in America, presumably came independently from Eurasia. Elaeocarpaceae are represented in Asia and the Pacific Islands, tropical America, and on Madagascar, where there are two species of *Elaeocarpus* and one of *Sloanea*, large genera widespread in Asia (see p. 579). *Weinmannia* and the group of genera including the Mascarene "*Macadamia*" have similar patterns of distribution. For each of these groups, depending upon a detailed analysis of distribution, one could perhaps most logically suggest that they may have reached Madagascar from the east, and need never have been present on the mainland of Africa, but it is very difficult to be certain.

Other disjunct groups have ranges which strongly suggest extinction in Africa. These include *Rheedia*, with about 15 species in tropical America, about 12 on Madagascar, and one in the Comores; *Phenax*, with about 25 species in tropical America, 3 on Madagascar; *Ravenala-Phenakospermum*; Liliaceae-Herrerieae (Herreriaceae); the ceroxylid and chamaedoreoid palms; *Rhacoma*; *Oplonia* (Acanthaceae); and *Oliganthes* (Asteraceae), all completely confined to Madagascar and the neighboring islands and tropical America at the present time. Animal groups with similar relationships are discussed by Paulian (1972: 11). For these groups, it seems likely in all cases that they were once present on the African mainland, and subsequently have become extinct there. Direct dispersal between Madagascar and tropical America seems a virtual impossibility, and the present ranges of these plants, together with a consideration of the climatic trends in Africa during the Tertiary and subsequently, appears to lend credence to a hypothesis of extinction on Africa in response to spreading drought.

For groups now more widespread, consideration of the relationships of the taxa involved may lead to an inference of whether they have become extinct on the mainland of Africa or not. For example, in Winteraceae, discussed on p. 563-4, long-distance dispersal is apparently not difficult, judging by the fact that *Tasmannia* has reached the Philippines since Miocene time. If the single species on Madagascar is in fact a *Bubbia*, an otherwise Australasian genus, then one might imagine that it reached Madagascar by long-distance dispersal. If on the other hand it is related to the exclusively New World *Drimys*, a possibility that has yet to be examined in detail, it might be a remnant of an ancient population of Winteraceae that extended across West Gondwanaland. Economy of logic at present suggests that Winteraceae may be an Australasian group that reached Madagascar by long-distance dispersal and America from Australia via Antarctica (Raven & Axelrod, 1972); but the alternate hypothesis also needs to be examined. For Proteaceae, discussed above, it appears very likely that ancestral Macadamieae, and specifically the ancestors of the group of four genera including *Brabeium* (South Africa), *Macadamia* (Australasia to southern tropical Asia, one supposed species in Madagascar), and the tropical South American *Panopsis* and *Roupala* (Johnson & Briggs, 1963), were once more widespread in Africa and migrated directly between Africa and South America. Monimiaceae s. str. have similar complex patterns of interrelationship involving the genera of Madagascar and neighboring islands and those of tropical America, strongly suggesting extinction on the mainland of Africa following direct migration between Africa and South America.

For Chloranthaceae, since the monotypic Mascarene genus *Ascarinopsis* is apparently not directly related to the American *Hedyosmum* but is similar to the Polynesian *Ascarina*, we suggest that the ancestors of *Ascarinopsis* reached Madagascar by long-distance dispersal from one of the other lands bordering the Indian Ocean. One may also argue by analogy that the apparently relict endemic taxa on Madagascar and neighboring islands, such as Didymelaceae, Medusagynaceae, Sphaerosepalaceae, Didiereaceae, Sarcolaenaceae, and dozens of genera and suprageneric taxa, may also have occurred at one time on the mainland of Africa, although this can be proved only if fossil evidence is found.

The geological evidence already reviewed, together with that from a history of the vertebrates, indicates little interchange of plants and animals between North and South America before Neogene time. For taxa that are well developed and apparently of some antiquity in South America, including some disjunct to Asia, the possibility exists that they have come *via* Africa and subsequently became extinct there. Again, such extinction can be proved only by fossil evidence from Africa, but the possibility needs to be weighed against others for the groups concerned, which have been reviewed in the pages above. These include Dipsacales (ancestor of Calyceraceae), Lardizabalaceae, Symplocaceae, Theaceae–Bonnetioideae, Rosaceae–Quillajeae s. str., Asteraceae–Mutisieae, the *Argylia–Incarvillea* line (Bignoniaceae), *Bambusa*, and *Meliosma* subg. *Meliosma*. For many of these groups, and for other disjuncts noted by Steenis (1962), the alternative hypotheses often seems no more likely than extinction in Africa: a very early arrival in North America followed by unlikely, very long-distance dispersal to South America, and sometimes by extinction in North America; or trans-Pacific long-distance dispersal. What we are urging here, as in the analysis of the affinities of the plants and animals of Madagascar and its neighboring islands with those of Latin America, is an awareness of the possibilities and an unprejudiced evaluation of the similarities.

The Cape Region of South Africa seems also to provide a refuge for certain plants and animals once more widespread in Africa, including *Brabeium*, the leptodactylid frog *Heleophryne*, and possibly the Proteaceae–Proteoideae and Restionaceae. That the African flora has been impoverished only recently is also implied by the history of the Canary Island laurel forest (Takhtajan, 1969: 203; Bramwell, 1972). Whereas this forest includes four genera of Lauraceae (*Apollonias*, *Laurus*, *Ocotea*, *Persea*), there are only five on the entire African continent. The Canary Island laurel forest inhabits middle altitudes (2,000 to 4,000 feet), chiefly on the north coast of the islands, where they are in the trade wind belt and hence are shrouded in fog during the hot summer months. A highly equable climate (see Axelrod, 1966: fig. 9) and ample fog-drip during summer help maintain the forest which clearly is a remnant of the much richer evergreen forest that covered parts of Europe and Africa in the Tertiary, and which is closely allied to the Afro-montane forest of the present day.

As judged from the fossil flora of southern Europe and north Africa, a similar forest persisted at sea level in southern Europe into the Late Pliocene (Depape, 1922; Bramwell, 1972), but it was eliminated there by colder glacial climates and by the spread of aridity over the Mediterranean and adjacent Africa during the drier inter-glacial ages. The persistence of laurel forest on the Canary Islands owes largely to fortuitous tectonic events. The low, semi-desert eastern Canary Islands (Fuerteventura, Lanzarote, Concepcion Bank) lie on the continental basement of Africa (Rona & Nalwalk, 1970). They are separated from it by a major northeast-trending strike-slip fault that has displaced the east Canary Island block 160 km southwestward from the Ifni gap, which it earlier occupied (Dietz & Sproll, 1970c). Apart from geologic evidence, the late Neogene remains of ratite birds on Lanzarote indicate that it was tied to Africa (Sauer & Rothe,

1972). Presumably as a result of movement of the east Canaries block, volcanism built up the western Canaries, composed of Tenerife, Gomera, Hierro, and La Palma which rest on oceanic crust. The oldest rocks are on Tenerife, and indicate volcanism from the Middle Miocene to Pliocene (16–4.5 m.y. BP). However, 80 per cent of the subaerial volcanism in the western Canaries is Pleistocene (2.0 m.y. and less), according to radiometric evidence (Abdel-Monem, Watkins & Gast, 1972). As the volcanos gradually increased in altitude, moist areas suitable for the forest came into existence. At levels above 2,000–2,500 feet a fog-deck now formed regularly during summer to provide favorable sites for persistence of the laurel forest that had earlier inhabited the lowlands nearby, but was disappearing there as precipitation decreased during the Pliocene.

The greater diversity of the Tertiary forest may be inferred from the geographic affinities of some of the taxa in the Canary laurel forest. For example, *Heberdenia*, *Drusa*, *Clethra*, and *Persea* are absent on the African mainland but have relatives in Latin America. In addition, there are the endemic genera *Visnea* (Theaceae), *Picconia* (Oleaceae), and *Bencomia* (Rosaceae), the latter belonging to a group that ties together Africa and South America, the tribe Sanguisorbeae.

As Richards has noted (1973), many of the species of the African rainforest are common and widely distributed, rather than rare and local as in the rainforests of America and southeast Asia. This situation finds a parallel in the flora of India, which also was left impoverished by spreading drought, and chiefly since the Oligocene (Axelrod, 1971). The Canary Islands, like Madagascar and to some extent the Cape Region of South Africa, provide refugia in which representatives of a formerly more widespread mesic African flora have survived in relative isolation and under the influence of an oceanic climate. These islands play for the ancient flora of Africa a role similar to that of New Caledonia and New Zealand with respect to the ancient flora of Australasia (Raven & Axelrod, 1972).

DISPERSAL BETWEEN WEST GONDWANALAND AND AUSTRALASIA

Geological evidence reviewed above suggests the possibility of more or less direct migration between Africa and Australasia up to the close of Early Cretaceous time— 110 ± 10 m.y. BP (Fig. 2). Although both the geological evidence and that from the distribution of vertebrates is inconclusive about when the connection between Africa and Australasia was severed, even the reconstruction at 75 m.y. BP (Fig. 2) suggests that Madagascar and India would have served as a subtropical route of migration, perhaps somewhat interrupted, to Australasia into Late Cretaceous time. Once the migration of tropical alliances by this route was no longer possible, Australasia was connected with the rest of the world only by a cool-temperate pathway to South America *via* Antarctica. Darlington (1957, 1965), Martin (1972), and others have argued that this corridor, judging from the distribution of modern organisms in South America, was unsuitable for many of the South American–Australian disjuncts. This is chiefly because a number of them now have tropical or subtropical patterns of distribution on both continents, as for example some of Proteaceae, discussed above.

Among the angiosperms, it is likely that *the ancestors* of the following ancient and archaic groups reached Australia in mid-Cretaceous time by a subtropical to tropical route from Africa:

Annonales, including the ancestors of Winteraceae and Monimiaceae st. str. and the suborders Magnoliineae and Laurineae. The other suborders and families may have evolved later, or in the Northern Hemisphere.

Balanopales.

Campanulales perhaps, if Goodeniaceae are closely related to Campanulaceae.

Casuarinales, its ancestors.

Commelinales, including the ancestors of several endemic Australasian families—Philydraceae, Centrolepidaceae, and Restionaceae. *Cartonema*, a very distinct genus of Commelinaceae, may have come subsequently.

Cornales, including Araliaceae and Haloragidaceae, as well as possibly *Phelline*.

Ericales, Epacridaceae.

Euphorbiales, including Thymelaeaceae and perhaps Euphorbiaceae.

Liliales, including the ancestors of the Xanthorrhoeaceae alliance, the Phormiaceae alliance, the Johnsoniaceae, the Asteliaceae, and Haemodoraceae-Conostyloideae.

Myrtales, Myrtaceae.

Pittosporales, as a part of Rosales (Cronquist, 1968).

Proteales.

Rosales, including Saxifragaceae subfamily Brexioidae and Cunoniaceae, in addition to ancestors of the endemic or sub-endemic Australasian taxa Eremosynoidae, Styliaceae, Cephalotaceae, Davidsoniaceae, Eucryphiaceae, and Corynocarpaceae, all of which are separately related to groups found outside of Australasia.

Santalales, including Santalaceae and Icacinaceae. The differentiation of Stackhousiaceae probably took place in Australasia after the early arrival of santalalian stock in the region. Olacaceae migrated to Australia by Paleogene time, became extinct, and re-entered subsequently.

Theales, including Dilleniaceae and possibly Hypericaceae, as well as the ancestors of Strasburgeriaceae and of *Oncotheca*.

An analysis of distribution patterns suggests that of Cronquist's (1968) six subclasses of dicots, only Magnoliidae and Dilleniidae-Rosidae (the distinction between them is becoming increasingly blurred; Eyde, 1974) were almost certainly in existence when more or less direct migration between West Gondwanaland and Australasia was possible. If the phytolaccaceous ancestors of Gyrostemonaceae came from South America *via* Antarctica, feasible considering the cool temperate Australian distribution of the group, and if the ancestors of Goodeniaceae-Brunoniaceae either did the same or reached Australasia subsequently by long-distance dispersal, then one could conclude from present distributions that neither Asteridae nor Caryophyllidae, nor their immediate ancestors, were in existence in mid-Cretaceous time. Although the relationships of Balanopaceae are obscure, *Nothofagus* and the Casuarinaceae probably provide an indication that Hamamelidae existed at that time, or soon after.

Among the monocots, Commelinales and Liliales are the only groups that seem likely, on the basis of present distributions, to have been in existence when more or less direct migration between West Gondwanaland and Australasia was possible. The monocots almost certainly originated in West Gondwanaland and many lines subsequently migrated to Australasia. It is very unlikely that any living genus of flowering plants is old enough to have migrated more or less directly between Australasia and West Gondwanaland, and there are at most only a few families involved in this pattern, which mainly concerns the ancestors of the groups we recognize as orders.

In general, the ease of migration to Australasia has decreased during the Late Cretaceous to Paleogene, only to increase again in Neogene time as the Australian plate neared Asia. Nevertheless, migration between Australasia and Africa *via* India and Madagascar probably was relatively direct, but with fairly long steps over water after the start of the Tertiary (65 m.y. BP). Among the taxa that seem, on the basis of their current representation, to be relatively old in Australia, but not as old as the mid-Cretaceous, are Araceae, Arecaceae (Eocene fossils), Celastraceae, Chenopodiaceae, Fabaceae-Faboideae, Loganiaceae, Oleaceae, Rhamnaceae, Rubiaceae, Smilacaceae, Sterculiaceae-Byttnerioideae, and Violaceae. Their ancestors may have arrived during Paleogene time, as probably also did those groups in which distinctive elements have evolved in Australasia: Bignoniales (Myoporaceae), Cornales (Haloragaceae), Chenopodiales (Gyrostemonaceae), Capparales (*Oceanopapaver*), Lamiaceae (Prostantheroideae), Liliales (Ripogonaceae), Verbenaceae (Chloanthoideae), and Malvaceae (*Plagianthus* group). *Canacomyrica*, a monotypic genus of New Caledonia which may be unrelated to Myricaceae (R. F. Thorne, personal communication), might also be placed in this list.

Nothofagus presents a special problem in its dispersal to Australasia. As suggested above (p. 573), the group of Fagaceae ancestral to *Nothofagus* may have spread to Australasia from the montane tropics by the mid-Cretaceous, using topographic highs on the Precambrian basement across Africa, India, and Antarctica which have since been largely reduced by erosion. The ancestors of the Australasian members of the suborder Magnoliineae (Himantandraceae, Eupomatiaceae, Degeneriaceae) may have done the same, since the only other member of the suborder is the essentially Laurasian Magnoliaceae. Similar problems are presented by many of the other groups in the list mentioned above, although their relatives in the Northern Hemisphere are often not clear. For example, the African Proteaceae and Restionaceae seem derived from Australasian progenitors; yet whence came the ancestors of the original Australasian stocks? In the absence of a more or less direct pathway from Asia into Australia in the mid-Cretaceous, we must postulate migration across Africa and India, followed by extinction, for many of these taxa.

Many plants and animals have certainly migrated between South America and Australasia *via* Antarctica (Raven & Axelrod, 1972), perhaps until Early Oligocene time. We emphasize, however, that this has not been the only possible route to Australasia during the history of the angiosperms. In Proteaceae, for example, some genera may have spread from Australasia to South America *via*

Antarctica, others went directly from Australasia to West Gondwanaland in the mid-Cretaceous (see discussion on p. 583–4), a duality of dispersal suggested earlier by Axelrod (1972c). Grevilleoideae have reached South America, probably by at least two different routes, and Africa; Proteoideae, Africa; and Persoonoideae, the most archaic of the three subfamilies, have remained in Australasia. If Restionaceae and Epacridaceae were truly present in the Eocene of southern England, they might have originated in Laurasia and reached Australasia by relatively long-distance dispersal. Restionaceae are evidently easily dispersed at present (Cutler, 1972), and it may be that their anatomically relatively homogeneous African representation arrived by long-distance dispersal across or around the Indian Ocean. Detailed consideration of individual families and other groups is necessary to determine their routes to and from Australasia.

For the vertebrates, there is no conclusive evidence that any group crossed Antarctica between Australasia and South America since Lower Triassic time (Colbert, 1972, 1973). Contrary to the view we expressed earlier (Raven & Axelrod, 1972), we now believe that the patterns observed among the vertebrates mostly suggest direct migration between West Gondwanaland and Australasia in the Jurassic and Lower Cretaceous. These groups include ratite birds, ceratodont lungfishes, osteoglossomorph fishes, rhynchocephalians (tuatara), leiopelmid frogs, and the ancestors of monotremes; all of these groups may have existed before the close of the Jurassic. Present evidence is inconclusive about the route by which meiolaniid and chelyid turtles reached Australasia, and about the route or routes whereby galaxiid fishes achieved their present Antarctic distribution.

Leptodactylid frogs seem certainly to have been present in West Gondwanaland, judging from present distribution and the occurrence of the endemic *Heleophryne* in Africa (Darlington, 1957; Cracraft, 1973b), and their occurrence in the Paleocene of India (Darlington, 1957). They may have reached Australasia directly *via* the subtropical route proposed above, although more comparative study of living and fossil anurans will be necessary before the question can be settled.

For marsupials, direct migration from West Gondwanaland to Australasia, with subsequent extinction in Africa, seems probable (Cox, 1970), and the age of the group appears compatible with such an hypothesis. Dispersal by this warm temperate to subtropical pathway answers Darlington's (1957, 1965) objections about the ecological requirements of marsupials. Further, the age of the dichotomy would be consistent with the great differences between Australasian and South American marsupials. Fossil evidence, especially from Africa, is highly desirable.

The distinctive placental mammals of West Gondwanaland may have originated after the marsupials (Lilegraven, 1969), and perhaps in Laurasia (Cracraft, 1973b), after the possibility of more or less direct migration between West Gondwanaland and Australasia had ceased. On this basis, the origin and composition of the mammal faunas of both South America and Australasia, as well as the relationships between them, would be neatly solved. The presence of a nearly complete (Dalziel *et al.*, 1973) land pathway between Australia and South

America would have presented an impassable filter bridge: cool temperate climate covered Antarctica from the latest Cretaceous onward (Raven & Axelrod, 1972).

Migration from West Gondwanaland to India and Australia by a warm temperate to subtropical route seems to provide a satisfactory solution for the anomalies in the distributions of dinosaurs we noted earlier (Axelrod & Raven, 1972). For example, the large dinosaurs from the Early Jurassic to the mid-Cretaceous of India indicate direct connections with Africa (Colbert, 1973), and Lower Cretaceous dinosaur faunas are in general of world-wide extent. Large sauropod dinosaurs, including the genus *Laplatasaurus*, are common to Argentina, India, and Madagascar in Late Cretaceous time. Dinosaurs entered Australia from other parts of the world in Upper Jurassic or Early Cretaceous time (Colbert, 1972), thus clearly demonstrating the efficacy of the warm temperate to subtropical West Gondwanaland–Australasian pathway, but unfortunately not telling us yet how long it persisted.

A major problem concerns the absence of not only marsupials but also monotremes, living and fossil, on New Zealand. We earlier inferred (Raven & Axelrod, 1972) that the arrival of marsupials in Australasia may have taken place subsequent to the separation of New Zealand from Australia–Antarctica (~ 80 m.y. BP), but this seems less probable in the light of the hypothesis advanced here. The dilemma is that many plants that do not seem to disperse across water gaps (*e.g.* *Nothofagus*, Proteaceae, austral gymnosperms) are well represented in the balanced flora of New Zealand, but there are few vertebrates. Ratite birds may be older, but why are there no living or fossil monotremes in New Zealand and why no reptiles, living or fossil, except *Sphenodon*? Although the question of direct Cretaceous land connections to New Zealand requires further study (Fleming, 1962, 1963; Gaskin, 1972), one or more shallow water gaps may have separated New Zealand and New Caledonia from Australia during the later Cretaceous. Current evidence indicates the Tasman Sea evolved by a process of seafloor spreading 60–80 m.y. BP (Hayes & Ringis, 1973). Hence, New Zealand and New Caledonia (Houtz *et al.*, 1973) were readily accessible only to the earliest immigrants.

Climate may also have been a critical factor. New Zealand, at latitude 60–70°S in the later Cretaceous (80 m.y. BP; Hayes & Ringis, 1973: fig. 7), would have had long dark nights and sustained low temperatures unsuited for most amphibians and reptiles, and probably early mammals as well. *Sphenodon* has extremely low body temperatures, ranging from a mean of 10.6°C (November) to 11°C (April), much lower than any other reptile (Bogert, 1953a, 1953b), and even lower than that reported for terrestrial salamanders (Brattstrom, 1963). Furthermore, tuatara has a lower metabolic rate than turtles and lizards. Its low metabolic rate and heat requirements may reflect its ancient Cretaceous (and earlier?) tolerance. On this basis, *Sphenodon* probably has survived in New Zealand because the area has had cool to cold temperate climates suitable for it continuously since the Cretaceous. Further, these climates could have been unsuited for other Cretaceous vertebrates, not only ectotherms, but endotherms

(marsupials, monotremes) may not yet have been able to withstand the sustained low yearly temperatures of New Zealand. In view of their absence, *Sphenodon* has been isolated from predators and has therefore survived.

We agree with Cox (1970), Fooden (1972), and others that marsupials may have become extinct in Africa, as have many other groups as discussed above. The views we have presented here appear to some extent to vindicate Darlington's (1965) skepticism about the importance of Antarctica as a route of migration for a number of megathermous groups of organisms, although for many microtherms it has certainly been of extreme importance. It is not possible to agree with Keast (1973) and Cracraft (1973a) about the unimportance of West Gondwanaland-Australian migration up to the mid-Cretaceous. This pathway provides a much simpler explanation for the distribution of many groups of subtropical requirements. If India provided a bridge from Africa to Antarctica and Australasia prior to Cenomanian time (Fig. 2), then the conclusion of Jardine and McKenzie (1972) that a route from South America *via* Antarctica was the only plausible one for marsupials obviously is invalid.

In concluding this section, we recall the crucial role that Antarctica has had in the history of land plants from later Paleozoic time onward. Antarctica was centrally located with respect to other austral lands from the Permo-Carboniferous well into the Early Cretaceous (Figs. 1, 2). It is this central position that accounts for the similarity of the *Glossopteris* flora at localities that are now as widely separated as India, Australia, Argentina, and South Africa (Plumstead, 1962; Seward, 1941: 178). Its central position also explains the close relationships between the Triassic and Jurassic floras of these austral lands, for they all share many species of ferns, seed ferns, cycadophytes and austral conifers (Seward, 1941: Tables B, C, D). As discussed in detail above, India-Antarctica served as a major route for dispersal of early angiosperms of warm temperate to subtropical requirements from West Gondwanaland to Australia. Furthermore, it served as a major pathway the temperate evergreen dicots and austral gymnosperms whose nearest descendants are now isolated in the Tasman and Fuegian regions (Axelrod, 1960: 270; Raven & Axelrod, 1972), taxa whose close relationships are "agreeable to the hypothesis of all being members of a once more extensive flora, which has been broken up by geological and climatic causes" (Hooker, 1853: 36).

As Antarctica moved to a more polar position during the Tertiary, forests were gradually eliminated there as temperatures were progressively lowered. Fossil floras from its borders (Snow Hill I., Seymour I.) and the Subantarctic Islands (Kerguelen, South Georgia, South Shetland, King George I.) suggest that forests were present on Antarctic into the middle Tertiary at least. Whether this is demonstrated by the pollen flora recovered at McMurdo Sound, Antarctica, (Cranwell *et al.*, 1960) is doubtful for it may have been carried there from distant lands: pollen of *Nothofagus* has been recovered from the modern peats of Auckland and Campbell islands, as well as Tristan and Gough! (Cranwell, 1963). Much of Antarctica seems to have been covered with a cool-temperate, evergreen forest into early Neogene time (Denton, Armstrong & Stuiver, 1971; Cracraft, 1973c). The leaf floras clearly indicate cold temperate equable climate like

that now in southern Chile and southern New Zealand. By analogy with the zonation of vegetation in these regions today, with a slight rise in altitude on Antarctica during the middle Tertiary, fern-bush and then rosette (tussock-cushion) communities would soon have appeared, and then permanent ice fields at altitudes near 3000–4000 feet, reaching down as ice tongues to the sea—as other data now also indicate (Hayes *et al.*, 1973). With further chilling as the ice fields continued to grow, there was a progressive retreat of evergreen forest, evergreen scrub and tussock-cushion communities, followed by their eventual extinction.

DISPERSAL BETWEEN NORTH AND SOUTH AMERICA

General.—Some 100 m.y. BP, in Turonian (Upper Cretaceous) time, South America and Africa were still in more or less direct contact. Until about 50 m.y. BP (early Late Eocene), when most modern angiosperm families and many genera were in existence, South America was closer to Africa than to North America, and hence more accessible to immigration from Africa than from North America. Subsequently, and especially since the Early Miocene (~ 26 m.y. BP), dispersal between North and South America has increased progressively. In the late Neogene, about 5.7 m.y. BP, these two continents were connected by land for the first time.

Putting it differently, South America has progressively rafted the plants and animals of West Gondwanaland toward North America. Many of the phylogenetic lines involved had earlier entered Eurasia from Africa, and then North America. As a result, a number of orders and families, and even some genera—*Meliosma* and *Persea* may be examples—were reunited when South America finally became attached to North America.

The fossil record.—Fossil evidence will eventually provide reliable information about the arrival of South American plants in North America and North American plants in the south. Interpretations of plant fossils are fraught with difficulty, however, and many of the older determinations are inaccurate and therefore misleading (see, for example, Dilcher, 1973, 1974). In view of the monumental work by Berry on the Cretaceous and Tertiary floras of North and South America, it is not possible to estimate quickly the validity of his paleobotanical taxonomy. Nonetheless, while it is certain that many of his identifications are in error, it seems unwarranted to regard his work as wholly worthless. His general picture of relations between the tropical to subtropical floras of North and South America seems reasonable, as may be judged from the following summary statement (Berry, 1937: 36):

“About 60 per cent of the genera, with over 100 species, are considered to have entered (the Gulf and Atlantic States) from equatorial America, either by way of Mexico, the Antilles, or as drift seeds and fruits.

“The climatic conditions on the east and west coasts of the Mississippi embayment resulted in considerable differences in the floras along the two shores. Thirty-three genera with 37 species are confined to the western shore, and 148 genera with 354 species are confined to the eastern shore.

The plants of the former show a greater resemblance to members of the contemporaneous floras of western North America and to the present day floras of central America; those of the latter are more closely allied to the present day floras of northern South America, and presumably entered the region, at least in part, by way of an extended Antilles."

The water barrier between North and South America was by no means an insurmountable obstacle for many plants. Sweepstakes dispersal readily accounts for the numerous taxa representing beach-jungle and mangrove vegetation in the Gulf and Atlantic States Eocene floras and provides a means for dispersal of taxa of more normal environments. In this connection, the present flora of the Indo-malayan region provides an excellent basis for judging the efficacy of migration. The flora now reaches eastward from Assam-Malaya to New Guinea, the Solomons and northern Australia, and north into the Philippines, forming a rather unified floristic region. It has been dispersed rapidly over islands that are spread at least twice the distance from the northern shore of South America to North America in Paleogene-Cretaceous time. Since there were scattered islands between Central and South America (Fig. 4), effective migration seems assured. Further, the distance is far less than that involved in dispersal to Hawaii, discussed above.

Distribution maps of typical tropical South American families (see Vester, 1940) show quite clearly that a number of them enter Central America only marginally, finding their chief centers of distribution in the Amazonian basin and bordering inner tropical regions. This is consistent with northward dispersal to their climatic limits at the edge of the inner tropics in Central America. However, it remains for future work to determine which of these may have arrived by long distance dispersal during the early or middle Tertiary, or moved north when a volcanic gangplank was finally constructed between the Americas during late Neogene time.

Eocene records of possibly South American plants from North America include those of MacGinitie (1969), who reports *Lomatia* (Proteaceae), *Anacardites* (supposedly directly comparable with the South American *Schinopsis*; Anacardiaceae), *Athyana* (Sapindaceae; South America), from the Eocene Green River flora of northwestern Colorado and northeastern Utah. None of these are now regarded unambiguously as valid records. The supposed *Athyana* probably represents Anacardiaceae (J. A. Wolfe, personal communication); the *Lomatia* record is not Proteaceae (cf. Johnson & Briggs, 1963); *Anacardites* is not necessarily most closely related to *Schinopsis*.

Other records reviewed by MacGinitie (1969) include the primarily South American or South American and African genera *Beilschmiedia* and *Ocotea* (Lauraceae) and *Swartzia* (Fabaceae). Records of the subfamilies Caesalpinioideae and Mimosoideae of Fabaceae and of *Bursera* (Burseraceae) are very interesting in the light of discussion presented in the present paper.

One significant record of a basically South American plant is a species of *Philodendron* sect. *Meconostigma* in the Middle Eocene of Tennessee (Daghlian & Dilcher, 1971, 1973; Dilcher, 1973b). Plants of this section are now confined

to subtropical South America and had been dispersed to North America at this early date. Dilcher (1973a) has shown that the Eocene floras of the Mississippi embayment existed under equable warm temperate to cool subtropical conditions, bordering on a seasonally dry to slightly moist temperature regime. *Dendropanax* (Araliaceae) is also reported from these deposits on the basis of a modern revision of the material, as are *Sabal* (Arecaceae), *Hura* (Euphorbiaceae), *Ficus* (Moraceae), *Ocotea* and *Nectandra* (Lauraceae), and *Podocarpus* (Podocarpaceae), all possibly austral groups (Dilcher, 1973b).

In a recent review, Leopold and MacGinitie (1972) consider that "Neotropical" elements were important in the Middle Eocene of the Rocky Mountain region and then became extinct by the Middle Oligocene. Among the genera they list are *Engelhardtia*, *Bernoullia*, *Thouinia*, and *Lindera*, which are tropical or warm temperate North American. Others which may have come from South America, with their times of first known appearance in North America, are:

Latest Paleocene—Cunoniaceae.

Early Eocene—*Annona* (Annonaceae), *Mabea* (Euphorbiaceae), *Luehea* (Tiliaceae), *Serjanea* (Sapindaceae), and *Oreopanax* (Araliaceae), all known from leaf fossils.

Earliest Middle Eocene—*Eugenia* (Myrtaceae) known from leaves; pollen of Sapotaceae and Bombacaceae.

Early Middle Eocene—*Apeiba* (Tiliaceae), leaves; pollen of *Ochroma* (Bombacaceae), *Guaiacum* (Zygophyllaceae), *Luehea* (Tiliaceae), Sapotaceae, tropical Meliaceae, *Iodes* and *Phytocrene* (Icacinaeae).

Late Eocene—Pollen of *Bombacopsis* (Bombacaceae).

On the basis of these records, Leopold and MacGinitie (1972) postulate a relationship of Middle Eocene Rocky Mountain flora with that of tropical America. Actually, many of the above records, and many others omitted here, can just as well be explained as survivors of an older, widespread subtropical Laurasian flora—a relation noted earlier by Berry (1937: 35). More reliable information from the fossil record will be necessary before it can be shown whether some or all of these taxa came from South America.

The analysis of the pollen flora of the Upper Oligocene San Sebastian Formation of Puerto Rico by Graham and Jarzen (1969; Graham, 1972) is of particular interest in interpreting the relationships between North and South America. Of the genera identified, *Podocarpus* (Podocarpaceae), *Acacia* (Fabaceae), *Aetanthus* (Loranthaceae), *Bombax* (Bombacaceae), *Brunellia* (Brunelliaceae), *Casearia* (Flacourtiaceae), *Catostemma* (Bombacaceae), *Chrysophyllum* (Chrysobalanaceae), *Corynostylis* (Violaceae), *Eugenia* (Myrtaceae), *Faramea* (Rubiaceae), *Guarea* (Meliaceae), *Jacaranda* and *Tecoma* (Bignoniaceae), *Marcgravia* and *Norantea* (Marcgraviaceae), *Pelliciera* (Theaceae), *Pleodendron* (Canellaceae), *Rauwolfia* (Apocynaceae) and *Tetrorchidium* (Euphorbiaceae) seem to be South American. This flora shows that by Upper Oligocene a number of South American taxa had crossed water barriers—most plausibly *via* Yucatan and Cuba—and entered Central America and the West Indies. The Cayman Ridge may have been largely above water in Early Paleogene time (Heezen,

Dreyfus & Catalano, 1973), providing more direct access to Cuba from northern Central America, as did the probable Eocene elevation of Yucatan above the sea. Relationships set up then, and the more direct accessibility of Cuba to immigration in Paleogene time, presumably provide the foundation for Alain's (1958) belief in a direct land connection. Such a connection does not in fact seem to have existed since prior to the Cretaceous, if then. Jamaica was submerged from the Middle Eocene to the Middle Miocene. The notion of a Paleogene arrival of some South American taxa in the West Indies would be consistent with the prominence of such groups as Cactaceae (Buxbaum, 1969), Gesneriaceae (*Gesneria*, *Rhytidophyllum*), and Canellaceae there. *Columnea*, with 11 endemic species on Jamaica, and *Alloplectus* (Gesneriaceae; Morley, 1972) provide examples of the kinds of genera that may have reached the North American area, including the West Indies, early in Neogene time.

Graham and Jarzen (1969) also reported three temperate North American genera in Puerto Rico: *Liquidambar* (Hamamelidaceae), *Nyssa* (Nyssaceae), and *Fagus* (Fagaceae). Geological evidence, as currently interpreted, does not support the great elevation of Puerto Rico in the Upper Oligocene visualized by Graham and Jarzen (1969), as pointed out by Graham (1972). Much more geological work needs to be done in this complex area, but the question of the paleoclimatic conditions under which temperate forest elements might have existed in Puerto Rico during Paleogene time must be considered further. R. A. Howard (1973, and personal communication) has pointed out that there are apparent remnants of temperate vegetation on a number of Antilles today, an observation which might assist in the interpretation of the occurrence of these temperate trees in Puerto Rico in the Oligocene. On the other hand, these remnants might have been derived from plant associations that spread between the islands by long-distance dispersal and achieved even greater extent during the cool, dry conditions obtaining during the Pleistocene pluvials and discussed above. It is just conceivable that the pollen was carried to Puerto Rico from another source: Germeraad *et al.* (1968: 206) have indicated that pollen from wind-pollinated trees in tropical montane vegetation is often carried over considerable distances, but it is not known whether these genera were present in Mexico before the Upper Miocene.

Although the present land connection between North and South America is only about 5.7 m.y. old, islands have allowed stepwise migration of plants in Oligocene, Eocene and perhaps even earlier times (Fig. 4). The Antillean Chain, however, is a more direct and complete pathway for migration at present than it ever has been in the past. To judge from the floras (Howard, 1973) and faunas of the Lesser Antilles, relatively few organisms seem to have used that route between North and South America—apart from beach-jungle taxa. The faunas and floras of the West Indies have certainly been accumulated across water barriers, as clearly stated by Darlington (1938, 1957) and many earlier investigators, and supported by the patterns outlined by Howard (1973). In the case of Jamaica, this only commenced in the past 15 m.y. For about the past 9 m.y., opportunities for migration from island to island, and to the group as a whole, have been maximal, with the exception that the possible Early Paleogene elevation of the

Cayman Ridge above the sea, discussed above, may have enhanced opportunities at the time for immigration, still across water barriers, into Cuba.

Among the plants from the Upper Miocene Paraje Solo site in Veracruz, Mexico (Graham, 1972, 1973a, and personal communication), are pollen grains identified as those of *Podocarpus*, *Faramaea*, *Fagus*, *Casearia*, *Liquidambar*, and *Guarea*, all reported from the Upper Oligocene of Puerto Rico (Graham & Janzen, 1969). In addition, there are members of the following families which appear to have been derived ultimately from South America: Polygonaceae (*Coccoloba*), Sapindaceae (*Matabya*), Thymelaeaceae (cf. *Daphnopsis*), Araceae (cf. *Spathiphyllum*), Chloranthaceae, Combretaceae, and Lecythidaceae. Other temperate elements include *Abies*, *Picea*, *Alnus*, *Celtis*, *Juglans*, *Myrica*, *Populus*, and *Ulmus*. By the Upper Miocene, therefore, elements of the temperate forest of eastern North America were well represented in the mountains of Veracruz (Graham, 1973a). In addition, a few grains of *Alnus*, *Juglans*, and *Myrica* have been found in the Miocene Gatun Formation of Panama.

As regards South America, *Juglans* was in Ecuador by the Uppermost Miocene (Brown, 1946), and other temperate North American genera for which documentation is available appear in northern South America in the Upper Pliocene and Pleistocene. *Alnus*, for example, appears suddenly at the start of the Middle Pleistocene in the Cordillera Oriental of Venezuela (Graham, 1972). Hammen (1972) records the appearance of *Alnus* (500,000 years ago) and *Quercus* (150,000 years ago) in northern South America following the Late Pliocene elevation of the mountains, together with the northward migration of such cool-temperate, southern genera as *Gunnera* and *Drimys*. These records support Chaney's (1936) view of a migration of temperate elements into Central America in Uppermost Neogene time, increasingly well documented by the studies of Hammen and Graham just reviewed. These studies suggest that at least a great majority of temperate North American plants did not appear south of the Isthmus of Tehuantepec until the Upper Miocene, at the earliest, whereas South American plants have become established in the tropical portions of the North American region from at least Eocene time onward, presumably by relatively long-distance dispersal over decreasing water barriers.

Evolution of a Latin American Biota.—Arguing from mammalian evidence, Simpson (1951: 407) reasoned that tropical North America would have been an important early site of evolution. His contention has been supported convincingly by Patterson and Pascual (1972), who point out that well over half the genera of Recent land mammals of northern origin in North America are found in the tropics, with about a quarter of the total only there—impressive figures when the present very limited extent of the North American tropics is taken into account. Considering that the tropics had a much greater extent in the Cretaceous and early Tertiary than at present, Patterson and Pascual seem almost certainly correct, although Whitmore and Stewart (1965) have argued that there was no tropical North American mammal fauna until the continent was physically joined with South America. Similarly, Darlington (1956), in part misled by erroneous notions of the relationship between Central America and North America in the Tertiary, contended that there was no truly tropical North American bird

fauna. However, most ornithologists maintain that such a fauna did exist and was indeed an important source of origin of many groups (*e.g.* Mayr, 1946; Bond, 1948; Cracraft, 1973c). Halffter (1964, 1972) has argued cogently that most of the insects of the tropical, as well as the subtropical and semiarid, portions of North America are ultimately derived from South America. Rzedowski (1972, 1973) has similarly allied a majority of the genera of flowering plants of the semiarid and arid regions of Mexico with those of South America, in addition to the more obvious connections among tropical plants.

From his detailed analysis of the Central American herpetofauna, Savage (1966) concluded that there is a unique and important endemic tropical element in Central America that is more or less independent of the North and South American faunas. He also indicated that tropical North America was an important early site of evolution for this group. As in many groups, Central America from at least the Miocene onward has been invaded by many new taxa of South American origin.

Generalizing, it now becomes clear why biologists have long been able to speak of a Latin American fauna and flora as if it were a unified whole (Simpson, 1950). For most groups—fishes, birds, amphibians, reptiles, insects, and plants are no exception—tropical North America, including Central America and the West Indies, has been populated mainly by a biota that evolved in isolation in South America. In some cases—birds, mammals, reptiles, certain plants—taxa that originated in tropical North America have become widespread in the New World tropics. In general, however, many of the North American plants that invaded South America in Pliocene time and more recently have temperate requirements and remained at high elevations or developed in the high latitudes southward in South America. The Pliocene elevation of the Cordillera Oriental that made migration of northern plants into South America more direct cut off direct migration from the lowland tropical Amazon Basin into Central America, as T. Croat (personal communication) has suggested. This event isolated the lowland rainforest west of the northern Andes from that east of the Andes for the first time. The tropical South American biota, which for plants began reaching North America in numbers in Paleogene time—the vertebrates later—gradually invaded the lowland tropics there. The Neotropical faunal region is thus recognized by the presence of basically South American animals, which have in some instances (*e.g.* armadillo) penetrated northward even to the deserts of the southwestern United States.

Thus the tropical biota of South America have progressively taken over areas of appropriate climate in North America (including Central America and the West Indies), just as the tropical biota of Asia have taken over the lowlands of New Guinea and neighboring islands, as well as northern Australia, while old Australian plants predominate in the more equable highlands (Raven & Axelrod, 1972). The spread of plants from South to North America, earlier and far more extensive than that of the vertebrates until the formation of an actual land connection, is also reminiscent of the situation in Australasia. Wallace's line, which divides the fauna of Asia from that of Australasia, is usually regarded as one of

the sharpest zoogeographic boundaries in the world; botanists, on the other hand, have tended to think in terms of an Assam-to-Fiji flora. This relationship has been discussed by Schuster (1972) and by Raven and Axelrod (1972), who relate it to the far greater dispersal powers of many plants than of vertebrate animals (Axelrod, 1952*a*). In America, it seems certain that modern types of tropical South American plants were established in numbers in the West Indies and southern North America by Paleogene time, but they were not followed in large numbers by vertebrates until after the late Neogene (5.7 m.y. BP) establishment of the Panamanian land connection. The biota of tropical North America, Central America, and the West Indies probably is comparable to the biota that would have developed in Australasia if a direct land bridge from Malaysia through Java to New Guinea and Queensland had been established in late Neogene time. Wallace's line would then presumably be much less distinct both for vertebrates and also for other groups of organisms.

In the light of the preceding discussion, we present the following list of plant families that probably spread from South to North America in Eocene time or subsequently:

Aizoaceae	Hernandiaceae
Apiaceae–Hydrocotyloideae	Lecythidaceae
Balanophoraceae	Malpighiaceae
Basellaceae	Marantaceae
Begoniaceae	Marcgraviaceae
Bixaceae	Mayacaceae
Bromeliaceae	Monimiaceae s. str.
Canellaceae	Myristicaceae
Cannaceae	Myrsinaceae
Caryocaraceae	Opiliaceae
Chloranthaceae	Passifloraceae
Chrysobalanaceae	Podostemonaceae
Cochlospermaceae	Proteaceae
Combretaceae	Quiinaceae
Connaraceae	Siparunaceae
Coriariaceae	Spigeliaceae
Cunoniaceae	Strychnaceae
Cyclanthaceae	Trigoniaceae
Elaeocarpaceae	Triuridaceae
Eremolepidaceae	Tropaeolaceae
Erythroxylaceae	Turneraceae
Fabaceae–Mimosoideae	Viscaceae
Flacourtiaceae	Vochysiaceae
Gesneriaceae	Winteraceae
Gunneraceae	Zingiberaceae
Gyrocarpaceae	

Other families seem to have already been represented in the North American region by taxa derived from Eurasia when the other elements arrived from South /

America. These judgments are made either on the basis of present patterns of distribution and endemism, on the fossil record, or both. The families include:

Acanthaceae	Moraceae
Anacardiaceae	Myrtaceae
Annonaceae	Olacaceae
Apocynaceae	Oleaceae— <i>Menodora</i>
Aquifoliaceae— <i>Ilex</i>	Orchidaceae
Araceae	Poaceae—Bambuseae
Araliaceae	Polygalaceae
Arecaceae	Portulacaceae—Calandrineae—except <i>Talinum</i> ?
Asteraceae	Rhamnaceae
Bignoniaceae	Rosaceae— <i>Acaena</i>
Bombacaceae	Rubiaceae
Capparaceae	Rutaceae
Caricaceae	Sabiaceae— <i>Meliosma</i>
Caryophyllaceae— <i>Colobanthus</i>	Santalaceae
Celastraceae	Sapindaceae
Commelinaceae	Sapotaceae
Cucurbitaceae	Scrophulariaceae— <i>Calceolaria</i>
Ebenaceae	Simaroubaceae
Euphorbiaceae	Solanaceae—including <i>Solanum</i>
Fabaceae—Caesalpinioideae—only <i>Cercis</i> in north	Sterculiaceae
Hypericaceae	Theaceae—for example <i>Ternstroemia</i>
Icacinales	Thymelaeaceae—only <i>Dirca</i> in north
Iridaceae—only <i>Iris</i> in north	Tiliaceae
Lauraceae	Ulmaceae
Lythraceae	Verbenaceae
Meliaceae	Violaceae
Menispermaceae	Vitaceae

A few additional groups appear to have come principally from South America, but they are so well or distinctively represented by endemic elements in North America that they may well have arrived in North America by early Tertiary time: Cactaceae, Liliaceae—Allieae, Loasaceae, Martyniaceae, Nyctaginaceae, Tecophilaeaceae, Zygophyllaceae. Sarraceniaceae, with one endemic genus in the Guyanas and one each in eastern and western North America, might also be mentioned here, although their past history is totally unknown.

A few isolated, mainly small taxa of familial or infrafamilial rank (categories of Airy Shaw, 1966, used here) are now confined to tropical and subtropical North America, and chiefly to semiarid and arid regions:

Agavaceae—most subgroups	Garryaceae
Canotiaceae	Goetzeaceae
Crossosomataceae	Koeberliniaceae
Fouquieriaceae	Krameriaceae

Lennoaceae
 Picrodendraceae
 Plocospermataceae

Simmondsiaceae
 Stegnospermaceae
 Verbenaceae—Lithophytoideae

In addition, at least 68 genera of woody plants are endemic to the dry regions of Mexico and the adjacent southwestern United States (Rzedowski, 1962, 1973).

As compared with the past, the tropical area of North America is now extremely contracted. The taxa in the preceding list occur in semiarid or subhumid sites which are separated from similar arid sites in South America by the moist tropics. It is among the plants of semiarid or subhumid habitats that most of the endemics occur (Rzedowski, 1962, 1964, 1973), presumably because there has never been good opportunity for interchange between the biota of such areas in North and South America in the past (Raven, 1963).

The following taxa may not have been in South America prior to Late Miocene or Pliocene time and then may have spread there from North America as migration became more direct. The taxa marked by an asterisk (*) already seem to have been represented in South America when the new arrivals came from the north. An additional list of genera is given on p. 631–2.

Actinidiaceae—*Saurauia*
 Apiaceae—Apioidae, Saniculoideae
 Berberidaceae
 Brassicaceae
 Caprifoliaceae
 Caryophyllaceae—except *Colobanthus*
 Cistaceae
 Crassulaceae
 Cucurbitaceae*—*Cucurbita*
 Cyrillaceae
 Ericaceae*
 Fagaceae*
 Hippocastanaceae
 Hypericaceae*—*Hypericum*
 Juglandaceae—*Juglans*

Linaceae*—*Linum*
 Lythraceae*—*Lythrum*
 Magnoliaceae
 Myricaceae
 Papaveraceae
 Poaceae—Festuceae, Triticeae
 Primulaceae
 Rafflesiaceae
 Ranunculaceae
 Rosaceae*
 Saxifragaceae*—including all
 Saxifragoideae and Ribesoideae
 Symplocaceae
 Valerianaceae
 Violaceae*—*Viola*

Many of these are montane plants that presumably expanded in the newly elevated mountains and temperate climates of South America, a trend that has persisted throughout Neogene time and up to the present.

Judging from their affinities, the following taxa may also have gone from North America to South America. They are so well represented there it seems probable that they are not very recent arrivals:

Boraginaceae
 Clethraceae
 Gentianaceae
 Hydrophyllaceae
 Loganiaceae—*Buddleia*
 Onagraceae—*Fuchsia*

Plantaginaceae
 Polemoniaceae
 Scrophulariaceae
 Theophrastaceae
 Viscaceae

Even among these plants, there is little indication of a primary North American tropical element: most are derivative temperate groups. In addition, it is apparent that there are not so many primitive or generalized types of plants in the flora of North America as in South America. Furthermore, clusters of small families similar to those of North America occur in widely separated semiarid and subhumid regions around the world. Thus, in the Mediterranean Region are Biebersteinaceae, Cynomoriaceae, Globulariaceae, and Punicaceae; in the Cape Region of South Africa, Achariaceae, Aitoniaceae, Bruniaceae, Geissolomataceae, Grubbiaceae, Penaeaceae, Roridulaceae, and Stilbaceae; and in Chile and subandean South America, Aextoxicaceae, Calyceraceae, Gomortegaceae, Malesherbiaceae, and Nolanaceae.

DISJUNCTIONS BETWEEN NORTH AND SOUTH AMERICA

It is now clear that long-distance dispersal is involved in the range disjunctions between desert plants of the Monte of Argentina and neighboring areas and the Sonoran and Chihuahuan deserts of North America. The problem has been discussed by many authors, and recently reviewed by Solbrig (1972, 1973) and by Werger (1973). Even though dry areas do exist in the tropics, they only attained maximum extent in the drier phases of the mid-Pliocene and Quaternary. The meagre fossil record does not provide evidence for an arid corridor during the Tertiary (Graham, 1972), although more sampling should be done along the western sides of the continents. Prior to the Pleistocene, arid areas were much smaller, less severe, and more widely separated than they are at present. Hence, the concept of a "trans-tropic scrub" (Barbour, 1969), from which the present ranges of taxa such as *Larrea* may have developed, is unsupported by any evidence.

The idea that relatively long "jumps" are involved in the establishment of the North-South American desert disjuncts is in agreement with the observations that (1) they constitute only a small proportion of their respective floras, (2) the animals associated with them in their disjunct areas are almost entirely different, and (3) they are mainly self-compatible (Raven, 1963). In genera which seem to have migrated more or less directly between North and South America, bees and other associated insects are often closely related. *Cucurbita* (Hurd *et al.*, 1971), for instance, provides an excellent example of a genus in which migration to South America must have taken place nearly directly in Neogene times, as it has closely related oligoletic bees associated with it on the two continents. In general, however, the evidence concerning the bee faunas north and south of the tropics in the New World suggests an historic lack of direct dispersal between them (Hurd, 1972); no species of bee has a range similar to that of *Larrea*, for example. Virtually all plant taxa disjunct between the monte of Argentina and the Chihuahuan Desert of North America meet the criteria just enumerated and almost certainly attained their disjunct ranges by long-distance dispersal.

The data suggest strongly that most of the disjunctions in range of desert taxa developed in the Pliocene, and especially more recently, as land connections between North and South America were established and as the rising cordillera produced widespread "rain-shadow" effects. For plants of Mediterranean cli-

mates, the disjunctions may be mainly Pleistocene and Recent in age (Raven, 1963, 1971), although the vegetation types involved existed from the Middle Pliocene onward (Axelrod, 1948, 1973).

As outlined above (p. 609–11), ample evidence now indicates that semi-arid to arid climates were widespread in low tropical latitudes during the ice ages. On this basis, relatively rapid migration would have been greatly aided by the presence of open areas in the subtropics and tropics, in regions presently under a regime of moister climate and covered with rainforest. Coupled with the intense tectonism and accompanying erosion that caused the development of intermontane drier valleys and lee slopes, it seems clear that during the ice ages there were much broader connections across the low latitudes than exist today—which the record does show. These connections may have developed especially along the western sides of the Andes and of Central and North America, onshore from areas of cooler water, and fossil evidence should be sought in such regions. On the other hand, much of the savanna vegetation of northern South America east of the Andes may be Recent in origin (Wijmstra & Hammen, 1966) and may therefore not have functioned as dispersal routes during the Pleistocene, for which the evidence is ambiguous (Hammen, 1963).

The open and relatively dry areas that formed in now forested regions during the glacial ages may well account for many of the links that are found between the monte and the warm deserts of North America, as well as those between the steppe and grassland climates of the Americas. Furthermore, these widespread open environments in the deep tropics during the glacial ages provide a more reasonable ecological basis for the interchange of mammals, especially large grazing and browsing ones (horses, glyptodonts, ground sloths, camels) between the Americas than those which exist now (Stirton, 1950) or the ones which existed during Neogene time. The evidence reviewed for ice-age aridity in the tropics (p. 609–11) strongly suggests that they crossed *via* areas of open savannas and grasslands that reverted to rainforest as each glacial stage waned. Whereas the savannas of South America may have existed on a regional scale since Oligocene time (A. Graham, personal communication), the pampas of the far south, with their rich representation of festucoid grasses ultimately derived from North America, cannot be older than the Uppermost Miocene, a conclusion that is consistent with other evidence (Vuilleumier, 1971).

For bipolar disjuncts (Moore, 1972), suitable habitats have probably been available in the Southern Hemisphere for at least 5 m.y., and long-distance dispersal has clearly been involved. For montane species that have extended their ranges between the Americas by means of way-stations on mountaintops (Moore, 1972; Raven, 1973*b*), Pleistocene and more recent times have undoubtedly been the most favorable, with very long gaps between suitable habitats having existed earlier. Among the genera that may have reached South America in this manner from the Upper Miocene onward, and perhaps mainly during the Pleistocene or more recently are *Adenocaulon*, *Agrostis*, *Alnus*, *Anagallis* (*Centunculus*), *Anemone*, *Antennaria*, *Aphanes*, *Apium*, *Aster*, *Astragalus*, *Barbarea*, *Berberis*, *Cardamine*, *Carex*, *Clematis*, *Chrysosplenium*, *Deschampsia*, *Draba*, *Eleocharis*, *Empetrum*, *Epilobium*, *Erigeron*, *Festuca*, *Galium*, *Habenaria*, *Hypericum*, *Hypo-*

choeris (despite its present absence as a native plant in North America), *Juncus*, *Lathyrus*, *Linum*, *Luzula*, *Oenothera*, *Orobanch*e, *Osmorrhiza*, *Poa*, *Polygonum*, *Potentilla*, *Potamogeton*, *Primula*, *Quercus*, *Ranunculus*, *Ribes*, *Rubus*, *Rumex*, *Salix*, *Sambucus*, *Sanicula*, *Saxifraga*, *Senecio*, *Trisetum*, *Urtica*, *Vicia*, *Viola*, and many other genera mentioned for example by Steenis (1972: 285–286). Moore (1972: 123–125) may have assigned too early a date to the arrival of some of these genera in the south, considering the past geological relationships between North and South America as now understood.

THE PLACE OF ORIGIN OF THE ANGIOSPERMS

Angiosperms could not have originated in the area that included Southeast Asia and northern Australasia to New Caledonia and Fiji, as earlier suggested by Smith (1967, 1970, 1973), Takhtajan (1957, 1969), and others. This region is a composite one geologically that came into existence only with the Miocene arrival of the Australian plate in the vicinity of Asia (Raven & Axelrod, 1972; Axelrod & Raven, 1972; Schuster, 1972). The persistence in Australasia of equable climates during the Tertiary, coupled with the increasing isolation of some of its components (*i.e.* New Caledonia, Fiji), has afforded some primitive angiosperms unusual opportunities for survival. The ancient unglaciated mountains of Southeast Asia, with their striking juxtaposition of temperate and tropical climates, are another such center of survival, as ably discussed by Takhtajan (1969) and Schuster (1972), and documented by the fossil record of the gymnosperms. Perhaps because many ancient and archaic angiosperms are adapted to moist, equable climates which would not have been likely over much of West Gondwanaland when Africa and South America were closely joined, and because of much extinction in Africa, they are better represented today in Australasia and Southeast Asia.

The *initial radiation* of the angiosperms certainly took place when direct migration was possible between South America, Africa, India, Antarctica and Australia, and *via* Africa to Laurasia, as is implicit in earlier investigations (*e.g.* Camp, 1947, 1952; Axelrod, 1952, 1960). In our present state of knowledge, North America does not appear to have been an important early site of differentiation of angiosperms, perhaps because of its limited access to tropical areas throughout its entire history. As to Australasia, our analyses indicate that it is an area to which various lines of angiosperms migrated following their origin elsewhere. In the interior of the vast continent formed by the union of Africa and South America would have been severe deserts (Axelrod, 1972*b*) and the sorts of semi-arid transitional areas that have been especially important as centers of plant evolution (Axelrod, 1952*b*, 1960, 1967, 1970, 1972*b*; Stebbins, 1952, 1972). Because of this, and since Southeast Asia seems to be an area of survival rather than of origin, we agree with Camp (1947), Schuster (1972), and others that angiosperms may have originated in Gondwanaland, but we particularly suggest West Gondwanaland. It is significant in this connection that Brenner (1974) has traced the Barremian-Cenomanian spread of tricolpate pollen from the northern part of West Gondwanaland northward during a period of some 25 m.y. to temperate Laurasia and finally the Arctic regions. See Addendum, Hopkins (1974).

Many of the mesophytic types of angiosperms now so well represented among archaic and ancient groups, generally regarded as primitive (Bews, 1927), may have come into being as West Gondwanaland split. With the accompanying spread of more moderate climates to which they became adapted, they then migrated to other parts of the world where similar climates occurred. In addition, just as Takhtajan (1969) argued that Southeast Asia was a likely place of origin for the angiosperms because of its crucial position in terms of contemporary routes of dispersal, we would argue that West Gondwanaland was centrally located on routes of dispersal at the time when the primary evolutionary radiation of angiosperms was taking place, whereas Southeast Asia at that time, widely separated from Australasia, certainly was not. In other words, given the geography of the mid-Cretaceous (Fig. 2), Southeast Asia is a very unlikely cradle for the angiosperms, contrary to the arguments of Takhtajan (1969).

Reasoning from the present distribution of the Annonales, Smith (1970, 1973) suggested that angiosperms—except perhaps for Annonaceae—may not have been present in West Gondwanaland prior to the separation of Africa and South America. However, the evidence presented here has revealed the existence of many links, among Annonalean families as well as other groups, between the floras of Africa and South America. In addition, there is the well known discontinuity in range for many taxa between the American and Asian tropics (Vester, 1940; Steenis, 1962; Good, 1964; Thorne, 1973). This pattern has resulted in part from the extinction of many angiosperm families in Africa. The relatively weak representation of primitive angiosperms in South America (Smith, 1967) may likewise find its explanation in the Neogene climatic history of that continent, as noted above.

If the environmental stresses that occurred in the dry interior of West Gondwanaland favored origination of the special features that make angiosperms—closed carpels, insect-mediated pollination systems, vessels, drought-resistant leaves, abundant secondary metabolites—then many of the most primitive lines might have become extinct as humid conditions spread in this area (Axelrod, 1970). A number of the secondary mesophytic lines might have become extinct later, with the spread of dry climates over the African sector and the elevation of mountains during the Tertiary. For these reasons, primitive angiosperms might not be so well represented as we might expect in areas where they appear to have originated.

There is a considerable amount of evidence that the invasion of these new habitats was the decisive step in the initial radiation of angiosperms, and was accompanied by the extensive formation of new polyploids (Stebbins, 1950: 359–369; Raven, 1975). As Takhtajan (1969) has pointed out, most primitive angiosperms are not in the tropical lowland forests but in the temperate mountains near these forests. A great majority of the existing families of Annonales and Hamamelidales are of polyploid origin, and these polyploid lines have evidently changed in their characteristics very slowly (see Stebbins, 1950: 359–369, for discussion). In contrast with Annonales and Hamamelidales, the Theales, a very primitive group which is well represented in both regions, do not display such extensive polyploidy as Annonales or Hamamelidales.

Suggestions can be made as to the place of origin of some of the major groups of angiosperms above the family level. Modern distributions suggest that the monocotyledons originated in West Gondwanaland; nearly all groups appear to radiate from, or are well represented in, that area. The superorder Annoniflorae of Thorne (1968), including Annonales and Berberidales, is extremely well represented both in the remnants of Gondwanaland and in Laurasia, as we have just discussed. The pattern in most other groups would be more consistent with an origin in West Gondwanaland than one in Laurasia, and indeed the pattern tends to agree with Cracraft's (1973*b*) analysis of vertebrates in the Old World: the phyletic lines in tropical Asia are in most cases derived. Hamamelidiflorae, including Hamamelidales, Casuarinales, Fagales, and doubtfully Balanopales, may, however, be a group that differentiated very early in Laurasia. Although the Casuarinales and Balanopales are Australasian and there are two genera of Hamamelidaceae in Africa, the superorder appears to be primarily Laurasian. The relationships of Casuarinales, and especially Balanopales, should be restudied, since they might be wind-pollinated derivatives of some other phylogenetic lines. For energetic reasons, and owing to intense herbivore pressure in the tropics (Heinrich & Raven, 1972), wind pollination has originated mainly in temperate regions. The wind pollinated members of Hamamelidales, Cistiflorae (Salicaceae), Urticales (Ulmaceae, Moraceae-Cannabinoideae), Rutiflorae (Juglandaceae, Myricaceae, Leitneriaceae), as well as many wind pollinated monocotyledons, have Laurasian distributions and doubtless originated there, where there is a much greater expanse of temperate lands than in the south. For wind pollinated plants, the warm tropics provide an almost impenetrable barrier (Heinrich & Raven, 1972), and Balanopaceae, Casuarinaceae, and *Nothofagus* are among the few well developed groups of wind pollinated dicotyledons south of the tropics. Ranunculanae (*sensu* Takhtajan, 1969) may also have originated in Laurasia, with Menispermaceae and Lardizabalaceae secondarily spreading to West Gondwanaland, presumably before the close of the Cretaceous. Most other major groups of angiosperms, however, seem to have had a long period of association with, if not their initial radiation in, West Gondwanaland.

In analyzing the history of any group, it is not possible to know where it originated; but we may learn where most of its early differentiation took place. For the angiosperms as a whole, and for both dicotyledons and monocotyledons, as well as for most of the major groups within these taxa, we suggest West Gondwanaland. This implies that the climatic changes that accompanied the breakup of this supercontinent, which commenced at about the time we first encounter angiosperms in the fossil record, may have been of critical importance in the evolution of the group and in the establishment of major lines within it. Africa-South America seems to be the homeland of the angiosperms, but it is a homeland devastated by subsequent geologic and climatic events, and one where access to temperate regions has been interrupted for most of the Late Cretaceous and Tertiary. Thus the primitive angiosperms, which may have spread initially into the equable, subtropical highlands, have survived in the greatest numbers in two regions where comparable habitats are ancient geologically and relatively well protected from immigration: Southeast Asia and Australasia.

SUMMARY AND CONCLUSIONS

West Gondwanaland was a primary area of evolution for many major groups, possibly including birds, marsupials, snakes, and anurans, but certainly many orders of angiosperms, and perhaps the earliest angiosperms themselves. The area included vast arid to subhumid tracts in tropical latitudes, terrain and edaphic conditions were diverse, and there was ample opportunity for rapid evolution. Opening the South Atlantic 125–130 m.y. BP, which signalled the spread of more mesic climates over much of the region, seems to have triggered the main evolutionary radiation and surge of angiosperms into the mesic lowland record ~ 110 m.y. BP. By the Paleocene, Africa and South America were separated by a gap of only ~ 800 km, populated with volcanic islands that aided east-west dispersal of tropical taxa.

The present-day amphi-Pacific tropical floristic similarities have resulted in many instances from massive extinction in Africa as a result of expanding aridity. This was brought on by increased elevation of Africa in the Neogene, by the appearance and gradual strengthening of the cold Benguela and Humboldt Currents during the Neogene, and by increased aridity over the inner African and American tropics during the glacial ages as the subtropic high pressure cells shifted equatorward and increased in strength. Many early “primitive” angiosperms were therefore eliminated from Africa and, in some instances, also South America, but have survived in tropical Southeast Asia and in northeast Australasia—areas of moist, equable climate relatively removed from the major vicissitudes of these Neogene and later climatic changes. The cyclic recurrence of aridity throughout the tropics during the glacial stages increased the areas of tropical savanna and grassland, and seems more nearly to explain the wide grasslands than repeated burning by early man.

The older biota of Australasia were acquired in or prior to medial Cretaceous time by more or less direct migration across Africa-Madagascar-India-Antarctica. These taxa of warm temperate to subtropical requirements included austral gymnosperms, a few orders and older families of flowering plants, and probably marsupials, dinosaurs, monotremes, ratite birds, ceratodont lungfishes, and osteoglossomorph primary freshwater fishes. Australasia remained open to immigration from South America by island stepping-stones for plants and animals of cool temperate requirements into the mid-Tertiary.

The general absence of land vertebrates from New Zealand–New Caledonia may reflect early isolation from Australia by a water gap. However, the cold climate and long dark nights that resulted from a high latitude position (60–70°S) may not have been suited yet for early mammals and most reptiles and amphibians. The very low body temperature and exceedingly low metabolic rate of *Sphenodon* may be symptomatic of the physiology of the group during Cretaceous and earlier times in cold latitudes.

We suggested earlier that separation of Australia–Antarctica in the Eocene resulted in the development and strengthening of the circum-Antarctic wind and current systems which have progressively increased the efficacy of long-distance dispersal across cold temperate austral regions, and this continues today. As Antarctica continued to move into deep freeze, increasing cold successively

eliminated evergreen dicot forests (Middle Miocene?), fern-scrub, and finally cushion-plant and herbaceous communities, with the latter now surviving in modified form on the scattered subantarctic lands, marginal to their home in the Pliocene and earlier.

India had a rich tropical to subtropical flora during the Cretaceous. In view of its direct contact with Africa and thence to South America, it is expectable that India has yielded fossil plants that are now confined to South America. Numerous genera of moist tropical Africa are now common to Southeast Asia. They linked Africa-India with that region during the later Cretaceous and Paleocene, when rainforest and savanna vegetation occupied the Tethyan shores and all of southern Eurasia. As the Indian subcontinent was rafted north through different climatic belts many tropical taxa unique to it appear to have been eliminated, as were temperate austral alliances, including leptodactylid frogs and austral gymnosperms. Their elimination left India with a rather general flora, characterized by few endemics as compared with other tropical regions. Spreading aridity in the Neogene and Quaternary further obliterated links to other tropical regions, and confined rainforest and savanna vegetation to the east at the expense of expanding thorn scrub, semidesert, and finally desert vegetation.

Many of the plants and animals that spread from West Gondwanaland (Africa) to Eurasia seem to have migrated subsequently to North America. Prior to the opening of the North Atlantic, and continuing into the early Paleogene, this was over generally low to middle latitudes and seems to account for the paleotropical element there. Direct migration between Europe and eastern North America following the early Paleogene was by increasingly cooler temperate biota as the North Atlantic widened. Although the direct interchange of mammals was blocked by the Eocene, balanced floras of progressively lower temperature requirements spread across these narrow water barriers throughout the rest of the Tertiary. Beringia, at higher latitudes during the Cretaceous and Eocene than at present, became increasingly important as a pathway between Asia and western North America. Generally warm temperate and subtropical biota utilized Beringia during the Paleogene, with mixed deciduous hardwood forests and conifer forests present in the lowlands, respectively, in the Miocene and Pliocene.

A 2,500 km water gap separated North and South America during Cretaceous and Paleogene time. The presence of volcanic archipelagos between them enabled plants to move generally north through the Cretaceous and Tertiary, but migration for most animal groups became regular only after the late Neogene land bridge was finally constructed. This bridge also enabled temperate montane plants in Central America to migrate into northern South America, as well as montane andine taxa to move into Central America, greatly increasing diversity there. During the Quaternary there was major long-distance, transtropic migration between areas of desert, steppe, and mediterranean climates in the Americas.

There are certain broad parallels in the later history of angiosperm floras of the Eastern and Western Hemispheres. The tropical lowlands of Central America and the West Indies, which increased markedly in area from later Paleogene time onward, have been populated by a tropical South American flora which predominates northward over much of southern Mexico. This finds a parallel in

a lowland flora of northern Australia–New Guinea which, although part of the Australian plate, has been populated almost exclusively by tropical taxa derived from the Asian tropics *via* the intervening islands. Also, the cordilleras of southern North America and of South America have been populated largely by temperate taxa derived from North America, as have the mountains of New Guinea by temperate Australasian taxa. During the latest Cenozoic there has been trans-tropic migration in each hemisphere, with a transfer of taxa from the colder boreal to austral areas.

Both in Australasia and in Africa remnants of the ancient flora have persisted on offshore islands separated from the mainland by seafloor spreading in the Upper Cretaceous and subsequently. The increasing isolation of these islands and their highly equable, oceanic climates have made them excellent sites for survival of ancient taxa.

It is amply clear that a restudy of the known Cretaceous and Paleogene floras of Africa–South America is a research project of highest priority. Previously described fossil floras should be intensively recollected, utilizing earth-moving equipment to secure adequate samples wherever possible. The taxa must be compared with those in the American, Malaysian, Australasian and African tropics and border areas, so that past links between these regions may be established wherever possible. The results should dispel at least some of our uncertainty about the early history of tropical floras, and of the angiosperms themselves.

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ADDENDUM: ADDITIONAL ANNOTATED REFERENCES⁴

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⁴ We are most indebted to Professor T. van der Hammen, Dr. G. F. W. Herngreen, Professor J. L. Langenheim, and Professor J. Muller for further advice and assistance concerning this paper.

- DALZIEL, I. W. D., M. J. DE WIT & K. F. PALMER. 1974. Fossil marginal basin in the southern Andes. *Nature* 250: 291–294.—In the southern part of South America a marginal basin opened behind an active andesitic island arc in the earliest Cretaceous and closed again in the middle Cretaceous.
- DINGLE, R. V. & R. A. SCRUTTON. 1974. Continental breakup and the development of post-Paleozoic sedimentary basins around southern Africa. *Bull. Geol. Soc. Amer.* 85: 1467–1474.—Sedimentation off the southeastern coast of Africa dates from the earliest rift (~180 m.y. BP) between East and West Gondwanaland. Sedimentation on the west coast dates from the opening of the South Atlantic, 125–130 m.y. BP. Subsequent major sealevel movements are attributable to epeirogenic/eustatic events that were probably worldwide in scope.
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- , J. H. WERNER & H. VAN DOMMELN. 1973. Palynological record of the upheaval of the Northern Andes: A study of the Pliocene and Lower Quaternary of the Colombian Eastern Cordillera and the early evolution of its High-Andean biota. *Rev. Palaeobot. Palynol.* 16: 1–122.—During the Early Pliocene, the central part of what is now the Cordillera Oriental was a tropical lowland, with small areas of savanna. The major ultimate uplift of the Cordillera took place during the Middle-Late Pliocene (4.5–2.5 m.y. BP). *Myrica* appears 3–2.3 m.y. BP, an open páramo-type vegetation about 2 m.y. BP. During the past 1.2 m.y., *Styloceras*, *Juglans* (>1 m.y. BP), *Alnus*, and *Quercus* appear in that order.
- HERNGREEN, G. F. W. 1974a. Palynology of Albian-Cenomanian strata of borehole 1-QS-1-MA, State of Maranhão, Brazil. *Pollen & Spores* 15: 515–555.—Close similarities between the Albian pollen floras of West Africa, the Maranhão Basin of Brazil, and Peru are discussed.
- . 1974b. Middle Cretaceous palynomorphs from northeastern Brazil. Results of a palynological study of some boreholes and comparison with Africa and the Middle East. "Sciences Géologiques" (Bull. Serv. Carte Géol. Alsace-Lorraine), Strasbourg, France

- (in press).—Evidence for continuous and clearly recognizable pollen zones from eastern Brazil *via* Central and North Africa to the Middle East (Israel and Saudi Arabia) from the mid-Albian to the Upper Cenomanian is in agreement with a post-Cenomanian separation of South America and Africa. The rich and diverse pollen flora of this region is very distinct from that found in Europe and North America at the same time, and includes among others *Psilatricolpites*, *Retitricolpites*, *Psilatricolporites*, *Hexaporotricolpites*, *Cretacaeiporites*, and *Tetradites*, found in the Middle and Upper Albian of Brazil and West Africa. It is apparently more diverse than the contemporary flora of Laurasia, an observation consistent with an origin of angiosperms in West Gondwanaland.
- HERRON, E. M., J. F. DEWEY & W. C. PITMAN III. 1974. Plate tectonics model for the evolution of the Arctic. *Geology* 1974: 377–380.—Extremely useful model consistent with the data presented in our paper.
- HOPKINS, W. S. 1974. Some spores and pollen from the Christopher Formation (Albian) of Ellef and Amund Ringnes Island, and northwestern Melville Island, Canadian Arctic Archipelago. *Geol. Surv. Canada Pap.* 73-12.—The assemblage of pollen and spores from the Albian indicates a moist, warm-temperate climate, with angiosperms with small and simple tricolpate grains appearing in mid- to Late Albian times, considerably before the Cenomanian records mentioned on p. 555 but still consistent with the notion of a poleward migration of the group.
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- LANGENHEIM, J. H., Y.-T. LEE & S. S. MARTIN. 1973. An evolutionary and ecological perspective of Amazonian Hylaea species of *Hymenaea* (Leguminosae: Caesalpinioideae). *Acta Amazonica* 3: 5–38.—As discussed on pp. 584 and 604, *Hymenaea* provides evidence for Paleogene drift across the ocean from Africa and South America. The tribe Cynometreae and probably the Caesalpinioideae as a whole seem to be of African origin.
- MANI, M. S. (EDITOR). 1974. Ecology and Biogeography in India. Dr. W. Junk, The Hague.—A useful collection of articles, the information in which should be assessed in terms of up-to-date chronologies of the movement of the Indian Plate. An article by Mani himself (pp. 614–647) is of particular interest in relation to the survival in India of biota of austral affinities and those which link India with Madagascar-Africa. The book contains very few references from 1970 and 1971, and none subsequently.
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- MATHUR, Y. K. & K. MATHUR. 1972. Angiospermous pollen and associated fossils from the Mid-Cretaceous subsurface sediments of Rajasthan, India. *Jour. Palynol.* 8: 89–96.—Angiosperm pollen from Albian, Cenomanian, Turonian, and Coniacian sediments indicate a wide diversity of angiosperms by Albian time, and it is claimed that these Cretaceous floras are more diverse than most contemporary ones elsewhere.
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- & L. DEL CASTILLO. 1974. Tectonic evolution of the southern Gulf of Mexico. *Bull. Geol. Soc. Amer.* 85: 607–618.
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- NAGLE, F. 1974. Blueschist, eclogite, paired metamorphic belts, and the early tectonic history of Hispaniola. *Bull. Geol. Soc. Amer.* 85: 1461–1466.—From pre-Cretaceous through Early Eocene time, Hispaniola was characterized by submarine basaltic and andesitic volcanism which ceased after the Paleocene or Early Eocene. Vertical uplift began during the Middle Eocene and has continued at least to Miocene time and perhaps to the present.
- PARMENTER, C. & D. W. FOLGER. 1974. Eolian biogenic detritus in deep sea sediments: A possible index of equatorial ice age aridity. *Science* 185: 695–697.—Confirms the pattern for glacial aridity in the tropics, specifically the southern Sahara.
- PRANCE, G. T. 1973. Phytogeographic support for the theory of Pleistocene forest refuges in the Amazon Basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalaceae and Lecythidaceae. *Acta Amazonica* 3(3): 5–28.—Proposed relatively extensive refuge areas are highly consistent with those of Haffer (1969), Brown (1972), and Brown and Mielke (1972), but not as restricted as those proposed by Vanzolini (1970).
- PRIMM, A. C., B. MCGOWRAN & S. GARTNER. 1974. Early sinking history of Ninetyeast Ridge, Northeastern Indian Ocean. *Bull. Geol. Soc. Amer.* 85: 1219–1224.—The Ninetyeast Ridge, a portion of the Indian Plate, rapidly sunk beneath the sea by the Maastrichtian and was at ocean depth by the earliest Tertiary. Evidence consistent with its rapid northward movement is presented.
- SAH, S. C. D. & R. K. KAR. 1973[1972]. Palynostratigraphic evaluation of the Lower Eocene sediments of India. Pp. 255–265, in A. K. Ghosh *et al.* (editors), "Proceedings of the Symposium on Paleopalynology and Indian Stratigraphy." University Grants Commission and Botany Department, University of Calcutta, Calcutta.
- SAHNI, A. & V. KUMAR. 1974. Palaeogene palaeobiogeography of the Indian subcontinent. *Palaeogeogr., Palaeoclimat., Palaeoecol.* 15: 209–226.—Oldest mammal fossils from the Indian subcontinent are from the early Middle Eocene, and they were derived from Asia.
- SANTAMARIA, F. & C. SCHUBERT. 1974. Geochemistry and geochronology of the southern Caribbean–Northern Venezuela plate boundary. *Bull. Geol. Soc. Amer.* 85: 1085–1098.—Hypotheses on the plate tectonics of the region which indicate a Late Cretaceous–early Tertiary period of intrusion and later metamorphism and a Late Eocene–Oligocene orogenic event, both reflected in the coast ranges of Venezuela. Fig. 13B shows volcanoes (Aves Ridge?) linking North and South America in the Late Cretaceous, as we have inferred.
- SAUNDERS, W. B., R. H. MAPES, F. M. CARPENTER & W. C. ELSIK. 1974. Fossiliferous amber from the Eocene (Claiborne) of the Gulf Coastal Plain. *Bull. Geol. Soc. Amer.* 85: 979–984.—Portions of the infrared absorption spectra of the amber are similar to those of *Shorea* (Dipterocarpaceae), but total spectrum is quite different and the identification seems as highly improbable chemically as it does botanically. We are indebted to J. L. Langenheim for her comments on this paper.
- SAVAGE, J. M. 1974. [Review of] Muller, 1973. *Science* 184: 685–686.
- SCHMINKE, H. K. 1974. Mesozoic intercontinental relationships as evidenced by bathynellid Crustacea (Syncarida: Malacostraca). *Syst. Zool.* 23: 157–164.—The relationships within this ancient group of freshwater Crustacea accord with what is now known about Mesozoic geography. *Notobathynella* of Australia and New Zealand is supposed to be less advanced than the two other related genera of Australasia, which also reach South America. This offshoot of the "*Chilobathynella*-group," now Asian, Australasian, and South American, presumably reached Australasia prior to the mid-Cretaceous, like many other groups. Movement was across an embryonic Indian Ocean, certainly not along a track such as that shown by Schminke in his fig. 5. This track did not exist until Miocene time, according to evidence from all other groups of organisms and available geological evidence.
- SCHNELL, R. 1971. Introduction à la Phytogéographie des Pays Tropicaux. Les Problèmes Généraux. 2 vol. Gauthier-Villars, Paris. Géobiologie, Écologie, Aménagement.—A valuable and detailed source book on tropical vegetation and plant distribution.
- SCLATER, J. G. & R. L. FISHER. 1974. Evolution of the East Central Indian Ocean, with emphasis on the tectonic setting of the Ninetyeast Ridge. *Bull. Geol. Soc. Amer.* 85: 683–702.—Suggests that India separated from Enderby Land in Antarctica about 100 m.y.

- BP, a conclusion consistent with the notion of a subtropical to warm temperate, possibly interrupted route of migration between Africa and Australia at that time.
- THORNE, R. F. 1974. A phylogenetic classification of the Annoniflorae. *Aliso* 8: 147–209.—In this important and useful paper, Thorne reduces Idiospermaceae (Blake, 1972) to a subfamily of Calycanthaceae, Idiospermoideae. As mentioned on p. 564 and 616 of the present paper, it seems reasonable to assume that primitive members of Thorne's suborder Laurineae migrated between West Gondwanaland and Australasia across a narrower Indian Ocean, and that the same might have been true for the ancestors of Monimiaceae, one of the families of this suborder. If the relationships postulated by Thorne are confirmed, the ancestors of Calycanthaceae *sens. lat.* might have done the same, which would imply their former presence and extinction in Africa. Thorne also divides Nymphaeaceae into five taxa, of which Nelumbonaceae (one bitypic genus with an impressive fossil record), Cabombaceae (monotypic), and Nymphaeaceae—Barclayioideae (monogeneric) are Laurasian. Of the other two subfamilies of Nymphaeaceae, Euryaloideae include the Asian *Euryale* and the South American *Victoria* and Nymphaeoidae include the cosmopolitan *Nymphaea* (represented by only a few species in Australia), the Laurasian *Nuphar*, and the monotypic Western Australian *Ondinea*.
- VENKATACHALA, B. S. & M. S. RAWAT. 1973[1972]. Palynology of the Tertiary sediments in the Cauvery Basin I. Palaeocene–Eocene palynoflora from the sub-surface. Pp. 292–335, in A. K. Ghosh *et al.* (editors), "Proceedings of the Symposium on Paleopalynology and Indian Stratigraphy." University Grants Commission and Botany Department, Univ. of Calcutta, Calcutta.
- WOPFNER, H., R. CALLEN & W. K. HARRIS. 1974. The lower Tertiary Eyre Formation of the southwestern Great Artesian Basin. *Jour. Geol. Soc. Austral.* 21: 17–51.—Documents increasing aridity from Eocene time onward, a trend consistent with the northward motion of the Australian plate.

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